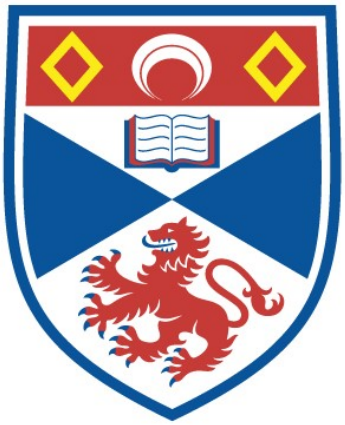
THE ROLE OF INDIVIDUAL BEHAVIOUR IN THE COLLECTIVE CULTURAL EVOLUTION OF HUMPBACK WHALE SONGS

Luca Ubaldo Lamoni

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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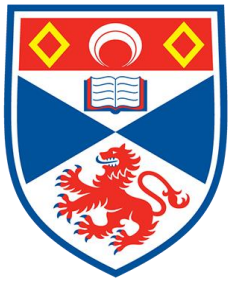

University of
St Andrews

This thesis is submitted in partial fulfilment for the degree of

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Digital Outputs access statement

Digital outputs underpinning this thesis are available at [https://github.com/MichaelMcloughlin/Humpback-ABM]

Contributions

Chapter 2

The coding of the models presented in chapter two was developed in collaboration with Michael Mcloughlin and resulted in a publication.

Mcloughlin, M.*, Lamoni, L.*, Garland, E. C., Ingram, S., Kirke, A., Noad, M. J., Rendell, L., Miranda, E. (2018). Using agent-based models to understand the role of individuals in the song evolution of humpback whales (*Megaptera novaeangliae*). Music & Science, 1, 2059204318757021. doi:10.1177/2059204318757021; *co-first authors.

Chapter 3

The starting model I used in chapter 3 is the one developed in chapter two in collaboration with Michael Mcloughlin. All the modelling updates introduced in chapter 3 were carried out by me, with input from Luke Rendell.

Chapter 4

All the song data analysed in this chapter have been collected between 2002 and 2003 by Michael Noad as part of the HARC project. Transcriptions were carried out with the help of three research assistants: Jennifer Coxon, Oliver Leedham and Malcolm Kennedy. I supervised and double checked all transcriptions. The rest of the analysis was carried out by me, with input from Ellen Garland.

General Abstract

For more than forty years, the complex songs emitted by humpback whales have fascinated the scientific community as well as the general public. These songs are produced by males during the breeding season, and are hierarchically structured and population specific. Within a population, males tend to conform to the same song type, but songs undergo gradual unidirectional change. Instances of more rapid song changes have also been recorded, where the song sung by a population has been replaced by the song of an adjacent population. The learning mechanisms that concurrently drive song conformity, and simultaneously allow gradual (evolution) and rapid (revolution) song change are not currently understood. This thesis aims to address this gap by using innovative theoretical models as well as more established empirical methods.

Chapter 1 provides a general introduction to the thesis topics. In chapter 2 I introduce a spatially explicit agent-based modelling approach to investigate humpback whale song evolution and transmission. I found that shared feeding grounds promote inter-population song transmission, song conformity emerges as a function of breeding ground geographical segregation, and production errors facilitate gradual evolution of songs. In chapter 3, the same modelling approach is extended to simulate song revolutions using a new learning bias in combination with different movement scenarios. I found that the consistent emergence of song revolutions is dependent on cognitive (song memory), behavioural (singing probability) and spatial (agent density) factors. Finally, in chapter 4, I analyse intra- and inter- individual song variability at different hierarchical levels of organisation in songs recorded off eastern Australia. I found that variability is not homogeneously distributed across the different song levels. Furthermore, I identified consistent and distinctive individual patterns of song production consistent with the theory that songs could represent mate quality advertisements for females.

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Chapter 1

General Introduction

In 1970 the biologist Roger Payne produced a best-selling environmental music album featuring the elaborate songs of humpback whales (*Megaptera novaeangliae*), which historically were subject of heavy whaling activity (Payne et al., 1970). This album was not only influential in raising awareness about this species' welfare, but it inspired the curiosity of generations of scientists that worked ever since to unveil the characteristics of this complex vocal behaviour. In a pivotal study, Payne and McVay (1971) described for the first time the complex hierarchical structure of humpback whales songs. The authors showed how individual sounds ('units') were grouped in 'phrases', how phrases were then repeated to form 'themes' and how distinct themes were sung sequentially, constituting a 'song'. Although the terminology defined by Payne and McVay (1971) to describe the different song components is still in use today, since the paper's publication in the early seventies more than 200 studies have also investigated the vocal behaviour of humpback whales (206 studies found using the Web of Science Core Collection Database with keywords: 'humpback', 'whale' and 'song'). Long-term monitoring effort led to understanding that within breeding populations song conformity is high and that songs are not static displays but undergo gradual changes (song evolution) over time (Payne et al., 1983; Payne and Payne, 1985). Furthermore, in some populations, changes can also occur more rapidly (song revolution) when a song is completely replaced by the introduction of a novel song from a nearby population (Noad et al., 2000). Together these observations provide substantial evidence that songs are culturally transmitted (Rendell and Whitehead, 2001; Laland and Hoppitt, 2003; Laland and Janik, 2006). Song types can be transmitted across populations over extremely large geographical scales, spanning the entire South Pacific (Garland et al., 2011). Cultural processes of such geographical and demographic magnitudes have been recorded otherwise only in human cultural evolution.

Although population-level song processes such as conformity, evolution, and revolution have been documented in the wild there is almost no information on the learning mechanisms that drive these cultural processes. Giving the impossibility of

captive studies and the large migratory range of this species, following individuals for long periods of time to test how songs are learnt, modified or replaced poses immense challenges. Therefore in this thesis the learning mechanisms behind the cultural evolution of humpback whales song are investigated using a bottom-up approach focused on the individual learning strategies involved in the collective behaviours seen in the wild. This is achieved by combining a new theoretical approach inspired by computer music research with analysis of songs from an extensive database of recordings made off eastern Australia.

1.1. Animal Communication

The ability to communicate is common to most of the organisms on Earth, including humans. Communication involves a sender, a receiver, and information that is transmitted via a transmission channel (typically the environment) by a signal (Bradbury and Vehrencamp, 2011). Communication can involve different sensory systems including the visual, chemical, electrical and acoustic apparatuses (Bradbury and Vehrencamp, 2011). Sensory systems and signals tend to co-evolve, forming specialised and complex communication systems (Osorio and Vorobyev, 2008). Sensory systems have evolved to increase the efficiency and reliability of signal reception and information extraction, in order to allow receivers to respond, either behaviourally and/or physiologically; concurrently, signals have evolved to increase broadcasting efficiency and the reliability of information decoding by the receivers, to the emitters' benefit (Endler, 1993; Endler and Basolo, 1998).

One way to classify signals is based on the context they are emitted in. Signals emitted in aggressive contexts might be used as threats, appeasement or indication of dominance status. Signals can reflect some feature in the environment, to communicate information regarding presence and/or location of food sources or predators. Social integration signals are used by group or communities to coordinate their behaviour during various activities such as foraging or migration. The last contextual category, which is the most relevant to this thesis, includes mating signals; these can be used activities such as mate attraction, intrasexual competition, and courtship (among others - see Bradbury and Vehrencamp, 2011). Mating signals are produced and received across

a wide range of modalities, including electrical (Hagedorn and Heiligenberg, 1985), chemical (Thomas, 2011), visual (Sivinski and Wing, 2008) and acoustic (Catchpole and Slater, 2008a). Acoustic signals represent one of the most effective means of communication in the animal kingdom, especially over large spatial scales. As with all other mating signals, acoustic displays can be subject to both intra and inter-sexual selection depending on which sex the signals are directed towards. Songbirds are a good example in which both selection processes can occur; males can sing to defend their territory from other neighbouring males as well as display the complexity of their vocal repertoire to advertise their fitness to females (Catchpole and Slater, 2008a). Acoustic communication is particularly relevant in aquatic environments, where the visual sensory system is limited by water turbidity and acoustic signals travel farther than in the air due to the medium's high impedance (Tyack, 1998; Bradbury and Vehrencamp, 2011).

Among aquatic organisms, marine mammals have some of the most complex and refined acoustic sensory systems. Acoustic signals are extensively used to communicate with conspecifics, maintain group cohesion, navigate and, in the case of odontocete echolocation, as a sensory modality. As a clade, marine mammals exploit a wide range of acoustic frequencies, from the infrasonic calls of blue whales (*Balaenoptera musculus*; Clark, 2004) to the ultrasonic whistles of spinner dolphins (*Stenella longirostris*; Lammers et al., 2003) and harbour porpoises (*Phocoena phocoena*; Clausen et al., 2010), to cite just few among many examples. A large number of experimental studies have demonstrated that cetaceans possess advanced vocal learning and cognitive skills, probably driven by complex social systems (Janik, 2014), in some cases resulting in cultural traditions that span generations (Slater, 1986; Whiten *et al.*, 1999; Noad *et al.*, 2000; Rendell and Whitehead, 2001; Laland and Janik, 2006).

1.2. Vocal Learning and Convergence

One of the modalities of social learning in humans and non-human species involves learning about acoustic signals; this particular form of social learning is known as vocal learning. Janik and Slater (2000) discriminate between two types of vocal learning (1) 'contextual learning', where individuals learn from conspecifics when to

produce a signal already in their repertoire, and (2) 'production learning', where signals are modified by the learner as a result of hearing other individuals' signals. Vocal production learning can lead to vocal divergence when there is pressure for vocal dissimilarity (Janik and Slater, 2000), but across many taxa it generally drives individuals towards vocal convergence.

An early example of vocal convergence in the bird literature is that shown by black-capped chickadees (*Parus atricapillus*). When free-living birds from four wild flocks were captured and rearranged in three experimental flocks, the calls of the members of each experimental flock significantly converged in their acoustic characteristics within a few weeks (Mammen and Nowicki, 1981; Nowicki, 1989). Examples of vocal convergence in birds have been documented in yellow-naped amazon parrots (*Amazona auropalliata*) (Wright, 1996), Australian magpies (*Gymnorhina tibicen*) (Brown and Farabaugh, 1991), Anna hummingbirds (*Calypte anna*) (Baptista and Schuchmann, 1990), male budgerigars (*Melopsittacus undulatus*) (Farabaugh et al., 1994; Hile et al., 2000), female budgerigars (Hile and Striedter, 2000) and finches (*Carduelis sp.*; Mundinger, 1970).

The evidence for vocal learning and convergence in adult mammals is patchy. Studies investigating vocal learning in bats, primates and cetaceans have produced some of the strongest results to date. Female greater speared-nosed bats (*Phyllostomus hastatus*) live in stable groups of unrelated individuals; they emit calls aimed to coordinate group members during foraging movements (Wilkinson and Boughman, 1998). Boughman (1998) showed how females modified their calls as a result of group composition changes, achieving an increased similarity among the new group members. There is also good evidence that vocal production learning plays a key role in bat pups' call development (Jones and Ransome, 1993; Esser, 1994; Knörnschild et al., 2009; Knörnschild, 2014).

Several examples from adult non-human primate studies suggest also that some degree of vocal production learning often leads to vocal convergence. Pygmy marmosets (*Cebuella pygmaea*) from two unfamiliar captive populations showed parallel vocal changes after being housed together for several weeks in groups (Elowson and Snowdon, 1994) or in pairs (Snowdon and Elowson, 1999). Similar group-specific

acoustic similarities have been documented for cotton-top tamarins (*Saguinus oedipus*) (Weiss et al., 2001; Egnor and Hauser, 2004), mouse lemurs (*Microcebus ssp.*) (Zimmermann and Hafen, 2001), Barbary macaques (*Macaca sylvanus*) (Fischer et al., 1998), and Japanese macaques (Sugiura, 1998). Evidence of some vocal production learning in adults has also been recorded for chimpanzees –for example, significant differences were found between the temporal patterning of pant-hoot vocalisations emitted by males from two captive colonies (Marshall et al., 1999). Genetic and environmental factors that could have affected the between-colony dissimilarity were ruled out, and in addition, a new pant-hoot variant was introduced in one of the two colonies resulting in five individuals acoustically converging towards this new variant. Wild chimpanzees seem to actively modify their pant-hoot vocalisations away from those of their neighbours (Crockford et al., 2004), and adjust their vocalisations to be more similar to the ones of their chorusing partners (Mitani and Gros-Louis, 1998). A more recent study showed that over the course of three years, immigrant adult chimpanzees displayed a gradual acoustic convergence over specific food grunts emitted by of the host captive group they were integrated with (Watson et al., 2015). None of these examples, however, concern the wholesale learning of new vocal utterances or sequences, which has long stood as something of a puzzle considering chimpanzees' phylogenetic proximity to language-learning humans.

Vocal learning underlies all the examples seen so far of vocal convergence, and cetaceans are a taxon in which the evidence for vocal learning is particularly strong (Janik, 2014). One of the most studied species, the bottlenose dolphin (*Tursiops truncatus*), has been the subject of both captive and wild studies and has proven to be an excellent study model to investigate vocal learning. Bottlenose dolphins develop individually distinct signals termed 'signature whistles' (Caldwell and Caldwell, 1965 ; Sayigh et al., 2007) used to convey the identity of the sender (Janik and Sayigh, 2013; King and Janik, 2013). Early studies conducted in captivity showed that bottlenose dolphins are capable of spontaneous whistle mimicry (Tyack, 1986; Reiss and McCowan, 1993) and can be trained to reproduce computer-generated 'model' sounds (Richards et al., 1984; Miksis et al., 2002). In the wild, signature whistle matching is predominant between close social affiliates, such as mother-calf pairs and male alliances (King et al., 2013; King et al., 2014; King and McGregor, 2016). Instances of vocal

convergence mediated by social affiliation have also been encountered (Smolker and Pepper, 1999; Watwood et al., 2004). Smolker and Pepper (1999) tracked changes in the vocal repertoire of three free-living male bottlenose dolphins over four years. Their acoustic repertoires at the beginning of the experiment were distinct but as these males formed an alliance their acoustic distinctiveness decreased. All three individuals converged on a set of similar whistle types (termed 'two-humps') and by the end of the experiment their most, and second most, commonly produced whistle was either of type 1 or type 2, both types were closely similar and presented the same frequency modulation characteristics ('two-humps' type).

Killer whales (*Orcinus orca*) show a similar predisposition for vocal learning and convergence. Studies of wild populations have documented stable vocal traditions over a period of 25 years (Ford, 1991), with several stable kin groups (pods) forming distinct acoustic associations (clans) characterized by unique acoustic repertoires; such vocal traditions were thought to be maintained through vocal learning (Ford, 1991). This hypothesis was later confirmed using genetic techniques (Yurk et al., 2002) as well as neural network methods (Deecke et al., 2000). Captive studies provided stronger evidence on killer whales' vocal plasticity compared to studies conducted on wild populations. Bain (1986) described cross-dialect unidirectional vocal convergence between two female killer whales (one from Iceland, one from the Pacific) housed together in the same facility. More recently, evidence for vocal production learning was provided by two studies in which captive killer whales reproduced the vocalisations of conspecifics as well as human sounds (Crance et al., 2014; Abramson et al., 2018).

An extensive body of work focused on sperm whale acoustic communication has unveiled the presence of large acoustic aggregations ('clans') that characterize the whales' population structure in the South Pacific. Rendell and Whitehead (2003) were able to allocate groups' vocal repertoires to five acoustic clans; clans incorporate several thousand individuals and span several hundreds of kilometres. Within-clan vocal convergence has profound implications on the whales' habitat use, movement patterns, reproduction rate and, ultimately, fitness (Whitehead and Rendell, 2004; Marcoux et al., 2007). More recently, multiple social units off the island of Dominica have been shown

to conform to a shared vocal pattern so completely that the units are indistinguishable in their production of it (Gero et al., 2016b).

As I have shown, the social learning of acoustic signals (vocal learning), while rare, is found in groups spread across a wide taxonomic range. Learning the utterances of conspecifics often leads to a process of vocal convergence. As shown in the examples above, vocal convergence can occur within dyads, within close social associates, within family groups and within larger unrelated groups. However, there is a species in which vocal convergence occurs at a surprisingly large scale. In humpback whales, all the males within a population conform to the same song type, even as this changes through time. The way humpback whale songs are learnt, how they vary geographically and how they are culturally transmitted across populations is going to be discussed in detail below.

1.3. Animal Culture and Cultural Transmission

The large body of evidence on animal vocal learning, convergence and geographical variability contributes to the current debate on animal culture. One of the first points of discussion within this debate is the very definition of culture. Some authors suggest that culture should arise only through teaching and imitation while accumulating modifications over time (Galef, 1992; Tennie et al., 2009). Other scholars decided to have a broader, more multidisciplinary definition in which culture can be referred as group-specific behaviours transmitted via social learning within a community or a population (Laland and Hoppitt, 2003; Whitehead and Rendell, 2015). Since the 1950s the term culture (or ‘sub-culture’ or ‘cultural transmission’ or ‘tradition’) has been cautiously introduced to describe examples of behavioural patterns in primates, such as potato washing and social grooming, and in birds, such as song dialects and foraging techniques (Fisher and Hinde, 1949; Kawamura, 1959; Marler and Tamura, 1964; McGrew and Tutin, 1978). However, a seminal paper that brought the animal culture debate to the attention of a wider and more multidisciplinary audience mapped the presence of 39 behaviour patterns across seven chimpanzee communities in central Africa, showing that different communities had distinct combinations of behavioural repertoires (Whiten et al., 1999). Two years later Rendell and Whitehead

(2001) widened the discussion by reviewing evidence of the presence of cultural processes in cetaceans, including instances of imitation and teaching in killer whales. While some authors insisted that there was not enough evidence for imitation and teaching to describe such phenomena as culture (Galef, 2001), others argued the exact opposite (Whiten, 2001).

One important point that has emerged from the animal culture debate is the difficulty in ruling out, experimentally, individual learning, ecology and genetic factors as the cause of the behavioural variations observed in the wild (Ripoll and Vauclair, 2001; Tschudin, 2001; Laland and Janik, 2006). For example, tool making has been described in several species including primates, marine mammals and birds. Depending on the species, this behaviour has shown to be influenced by individual learning (Tebbich et al., 2001), environmental factors (for example tool material properties; Klump et al., 2015) or social learning, as in the case of sponging in bottlenose dolphins (Krützen et al., 2005). A further example of the potential effects of genetic factors on vocal diversity was described across seven crested gibbon species (genus *Nomascus*). In this study the authors showed strong correlations between song structure and genetic similarity, and between song similarity and genetic distance (Thinh et al., 2011). These recent studies suggest that with improved genetic testing together with careful study design it is possible to identify and measure the influence that genetic, ecological or social factors could have in the variation of behavioural traits seen in wild populations.

Environmental, genetic and cultural factors do not however act separately in the evolution or development of a behavioural phenotype (Bateson and Martin, 2000). Since the 1970s the co-evolutionary relationship between genes and culture has been thoroughly investigated for humans (Feldman and Cavalli-Sforza, 1976; Feldman and Laland, 1996). In the late 1980s gene-culture coevolution theory was applied for the first time to the study of vocal learning in songbirds (Aoki, 1989).Ten years later Lachlan and Slater (1999) designed a new theoretical framework, based on a spatially explicit modelling approach, to test how genes and vocal learning could interact in an evolutionary scenario to maintain song learning in birds. Their simulations confirmed that song learning could be maintained across generations by the interaction between genes and culture even though it did not produce higher levels of fitness in the

population. More recent evidence supports the importance of gene-culture co-evolution in cetaceans, showing that the emergent speciation of killer whale ecotypes could be associated with socially inherited ecological niches, which include dietary specialisations that are usually culturally transmitted (Riesch et al., 2012; Foote et al., 2016; Whitehead, 2017). Another form of gene-culture co-evolution is cultural hitchhiking, where functionally neutral genes are transmitted in parallel with selectively advantageous cultural traits. It has been suggested that cultural hitchhiking could explain the low genetic diversity encountered in the control region of the mtDNA in the four cetacean species that have matrilineal social systems (Whitehead, 1998). Theoretical models have also shown that cultural hitchhiking is a plausible explanation in circumstances similar to the ones displayed by matrilineal societies such as sperm whales (Whitehead, 2005, 2017).

Theoretical research has been fundamental in the understanding of the cultural transmission processes that characterise both human and non-human species. Early models of human cultural transmission laid the foundation for many of the theoretical approaches that are used now; furthermore, they shed light on the adaptive value of behavioural conformity in spatially and temporally varying environments (Feldman and Cavalli-Sforza, 1976; Cavalli-Sforza and Feldman, 1981; Cavalli-Sforza et al., 1982; Boyd and Richerson, 1985; Henrich and Boyd, 1998). Theoretical modelling approaches have also been of key importance in the study the role of social learning and vocal conformity in birds. Models that run over multiple generations in spatially simulated territories have been used to study the evolution of vocal dialects, helping to formulate hypotheses that could be then tested in the field (Goodfellow and Slater, 1986; Slater, 1986; Lachlan and Slater, 1999; Lachlan and Slater, 2003). These initial efforts led to an ever-growing research effort that exploits different modelling approaches in order to study the effect of social learning strategies and social structure on the evolution of cultural transmission and maintenance of cultural traditions (Ellers and Slabbekoorn, 2003; Lachlan et al., 2004; Lachlan and Servedio, 2004; Sellers et al., 2007; Olofsson and Servedio, 2008; Rendell et al., 2010; Fogarty et al., 2012; Rowell and Servedio, 2012). Agent-based modelling is a technique that has seen an increased range of applications in recent years. In this simulation modelling approach a system is created containing a set of autonomous entities (usually referred as agents) that follow

predefined rules to interact with one another and with the environment. The model can then be used to study the bottom-up emergence of population level phenomena. Agent-based models have been applied to a variety of human and non-human systems (Bonabeau, 2002; Bousquet and Le Page, 2004; Macal and North, 2010; McLane et al., 2011). In the context of animal social learning and culture, a recent study demonstrated the power and versatility that a theoretical approach using agent-based models can achieve when well informed by real data. Cantor et al. (2015) investigated the origin of vocal clans in sperm whales using an agent-based model informed by empirical long-term data. The results indicated that the upper social level of sperm whale multilevel society (i. e. the vocal clans) emerged when agents culturally acquired the most common codas (that is, they showed a conformist bias) from behaviourally similar agents.

Such uses of a theoretical approach to study cultural transmission can be extremely beneficial when the target species cannot be studied in captivity. This is especially true in cetaceans given the large geographical and temporal scales on which they live. Field studies are challenging, researchers are usually limited to a narrow time window to perform their experiments, and usually it is impossible to follow an individual over sufficiently long time scales to adequately capture their developmental trajectories. Given these considerations, humpback whales represent a great candidate for theoretical studies on animal culture. As I will explain more thoroughly in the next sections, humpback whales represent one of the clearest examples of cultural transmission in the animal kingdom (Noad et al., 2000; Laland and Hoppitt, 2003; Laland and Janik, 2006; Garland et al., 2017a). Male humpback whales produce long, complex and stereotyped sound sequences defined ‘songs’ (Payne and McVay, 1971) predominantly, but not exclusively, during the migration and the breeding season. Within a population, males display a high degree of song conformity (Cholewiak et al., 2012) and songs can be transmitted across multiple populations over entire ocean basins (Garland et al., 2011). While population level song conformity has been recorded in multiple humpback whale populations, the role of individuals in the cultural evolution and transmission of songs remains unclear.

1.4. Humpback Whales

1.4.1. Distribution, Movement and Ecology

Humpback whales are distributed across all oceans. The International Whaling Commission (IWC) defined seven distinct humpback whale breeding stocks in the Southern Hemisphere - named with letters A to G. These breeding stocks migrate between low-latitude breeding grounds and six high-latitude feeding grounds off Antarctica in the Southern Ocean (areas I to VI; IWC, 2006), usually displaying high site fidelity to natal breeding grounds (Baker et al., 1998). The Northern Hemisphere hosts three main populations (and several sub-populations) in the northern parts of the Pacific, Atlantic and Indian Oceans respectively; whales in this hemisphere tend to display high site fidelity towards their feeding grounds while populations (or sub-populations) overlap in shared breeding grounds (Palsbøll et al., 1997; Calambokidis et al., 2001). In the Southern Ocean, due probably to the different geography (i.e. the absence of physical barriers around Antarctica), humpback whales seem to follow the opposite pattern, overlapping in the feeding grounds and segregating in geographically distinct breeding grounds (Olavarría et al., 2007; Schmitt et al., 2014; Rosenbaum et al., 2017).

Female humpbacks generally give birth during the breeding season in warmer, more protected low latitude waters (Clapham, 2000). Sexual and physical maturity are reached at 3-6 and 10 years respectively (Chittleborough, 1965). Females are slightly larger than males and they are seasonally polyoestrous, with their gestation lasting approximately 11 months; lactation lasts on average 10.5 months and shortly after (generally one year) mothers and calves separate (Chittleborough, 1958; Clapham and Mayo, 1990). The timing of migration is usually dependent on the sex and age of the individuals. Lactating females tend to be the first reaching the breeding grounds followed by immatures, mature males, non-reproductive females, and finally pregnant females (Chittleborough, 1965). In the breeding grounds and along migration humpback whales tend to associate in unstable, often competitive groups, where males display aggressive behaviours in order to escort, and potentially mate, with females that are both with and without calves (Tyack and Whitehead, 1983; Baker and Herman, 1984;

Clapham et al., 1992). Humpback whales produce different types of vocalisations: those that are called ‘social sounds’ produced by males and females (Tyack, 1983; Dunlop et al., 2007), some recently reported ‘megapclicks’ associated with feeding events (Stimpert et al., 2007), and complex stereotyped sequences of sounds defined as ‘songs’ (Payne and McVay, 1971), emitted only by males (Winn and Winn, 1978; Tyack, 1981). In the next sections I will describe the structure of songs, their potential function, their geographical variability and finally, their cultural evolution.

1.4.2. Song Structure

Hierarchical structure is one of the most characteristic features of humpback whale songs. The basic element of the song is the unit, which is defined by Payne and McVay (1971) as ‘the shortest sound that seems continuous to the human ear’. Units vary widely both in the temporal (i.e. duration) and the frequency domain, ranging from a few hundred Hz to harmonics of more than 20 kHz (Au *et al.*, 2006). Payne and McVay (1971) reported the presence of distinguishable signal components such as inflection points and frequency discontinuities, defining them sub-units. Pace et al. (2010) proposed sub-units as the basic constituent of songs, rather than the more complex units, using an energy detector and a clustering algorithm to classify them, but this interesting idea has not yet been followed up.

The next level up in the hierarchical organisation of songs is the sub-phrase. A sub-phrase is constituted by a combination of one or more units; if only one type of unit is repeated the sub-phrase is defined as ‘similar’, if two or more units are repeated in combination several times then the sub-phrase becomes ‘dissimilar’ (Cholewiak et al., 2012). A sequence of multiple sub-phrases forms a phrase, which is usually repeated several times before the introduction of a different phrase. Payne and McVay (1971) defined phrases as ‘inexact replicas’ of one another. For example, in a repetitive sequence of a single phrase type the unit number within each phrase might vary slightly across the repetition sequence. Phrases are defined by the specific sequence of constituent units, and not by their time domain characteristics, because the intervals between phrases and between units within phrases are generally similar (Cholewiak et al., 2012). Phrase duration is one of the most stable features of humpback whale songs,

with an apparent low coefficient of variation within and between individuals (Cholewiak et al., 2012). Phrase composition can vary in time; it is also possible to find 'transitional phrases' (Cholewiak et al., 2012) or 'hybrid phrases' (Darling et al., 2014) which combine units from two different phrase types.

A theme is composed by the repetition of the same phrase, thus if a new phrase type occurs then a new theme is started (Payne and McVay, 1971; Frumhoff, 1983). Contrary to phrase duration, theme duration appears to be quite variable both within and between individuals; whales can sing different numbers of phrases, even in consecutive renditions of the same theme (Cholewiak et al., 2012). Payne and Payne (1985) grouped themes into three categories: (1) static themes, which always display sequences of identical phrases; (2) shifting themes, in which phrases change progressively (principally in frequency, duration, and production rate) across the theme rendition, and lastly (3) un-patterned themes that display a variable number of units with poor phrase organisation. Other studies have suggested the presence of 'fundamental' themes (Frumhoff, 1983; Chu and Harcourt, 1986), which were themes present in at least 90% of the recordings in both a given and a contiguous season (Frumhoff, 1983; Chu and Harcourt, 1986). However, themes are not static, they vary (evolve) through time (Payne et al., 1983), therefore the definition of 'fundamental themes' is of questionable value (Cholewiak et al., 2012).

A song is a sequence of distinct themes (Payne and McVay, 1971). It is usually decided arbitrarily which theme initiates the song, even though sometimes the song sequence begins with a dive and ends at the next surfacing period (Darling et al., 2014). Song bouts, in which multiple song cycles are performed, can last several hours; in an extreme example a male produced a 22 hour song bout without interruptions other than breathing (Winn and Winn, 1978). Considering the variability in theme duration, it is not surprising that song duration appears to be extremely variable as well; early estimates ranged between 6-7 min and 30-35 min (Payne and McVay, 1971; Winn and Winn, 1978). A more recent quantitative analysis narrowed down the range between 7.5 and 16.7 min (Suzuki *et al.*, 2006). Early studies suggested that the usual song structure was stereotyped and rigid with fixed sequences of themes (Payne and McVay, 1971; Winn and Winn, 1978; Payne and Payne, 1985). However, more recent studies show

that theme transitions can either be stable or variable depending on year and location (Cholewiak et al., 2012). More variable songs have been also defined as 'aberrant' (Frumhoff, 1983) and 'poorly structured' (Cato, 1991). A song 'type' is a sequence of themes sung by a given population at a given time and distinct from other such sequences (Garland et al., 2011), and this definition is extremely useful when comparing songs across both time and space.

During the past 40 years the hierarchical structure of humpback whale songs described by Payne and McVay (1971) has been widely accepted and confirmed both qualitatively and quantitatively (Suzuki *et al.*, 2006; Miksis-Olds *et al.*, 2008). Similar hierarchical structures have been described also for bird songs (Honda and Okanoya, 1999; Hosino and Okanoya, 2000; Suge and Okanoya, 2010; Berwick et al., 2011). A contrasting theory attributes the acoustic regularities recorded in humpback whale songs to the physical (water depth) and physiological (air recirculation) constraints of sound production (Mercado and Handel, 2012), but has received little support.

1.4.3. Song Function

Sexually selected traits are usually possessed by males and used by females to select a mating partner, or by males for intrasexual competition for mates, or both (Bradbury and Vehrencamp, 2011). These traits can be subject to a runaway evolutionary pressure if they are positively selected for no other reason than their role in mate competition, resulting in excessive and complex traits, like the exaggerated tail displays of peacocks (*Pavo cristatus*; Shahla and Yahya, 1996) and the large repertoire size of song sparrows (*Melospiza melodia*; Reid et al., 2004). Sexually selected behavioural displays can be costly to produce both in terms of time, that could be spent foraging, and energy, due to the fact that males can perform these displays for several hours on end (Bradbury and Vehrencamp, 2011). Humpback whale songs have several classic features of a sexually selected trait. Songs are emitted only by males, in bouts that can last up to several hours, and their structure appears excessively complex for a simple communicative function.

In early studies, humpback whales were recorded singing exclusively during the breeding season; as a result researchers hypothesised that songs were somehow part of

the mating system (Payne and McVay, 1971) and that potentially only males produced them (Winn and Winn, 1978; Tyack, 1981). Both hypotheses were later confirmed by several field studies (Helweg et al., 1992; Medrano et al., 1994; Smith et al., 2008). The evidence that songs play an important role in the whales' mating behaviour is now substantial, but there are different theories regarding the exact function of male songs (Herman, 2016). In the past, a few authors have tried to answer this question through playback experiments. Tyack (1983) described a differential response between song and social sound playbacks, recording avoidance in the former case and attraction in the latter. He proposed that songs might broadcast information related to sex, location and readiness to mate to both females and neighbouring competing males (Tyack, 1981). Other studies developed this hypothesis further, suggesting that specific song features might convey an indication of the singer's fitness and/or status to females and/or other males (Chu and Harcourt, 1986; Adam et al., 2013). Assuming that songs are directed toward females, males could also be using songs to create a 'floating lek' to attract females acoustically (Clapham, 1996). The participation of more singers could increase the average signal levels, possibly attracting more females and therefore increasing mating possibilities (Herman et al., 2013). Field studies in Hawaii, however, support an alternative hypothesis that songs play a role in male-male interactions, questioning the 'female-attraction' hypothesis (Darling and Bérubé, 2001). In the context of a dominance polygyny mating system (Brown and Corkeron, 1995) songs might function to organise male aggregation groups. For example, a focal singer whale approached playbacks of similar songs and avoided playbacks of different songs (Darling et al., 2012b). In a recently published study conducted in Mexico, males were recorded altering their song renditions when other singers were present - focal whales tended to switch themes more frequently in presence of other singing males, indicating that songs have a role in mediating intrasexual interactions (Cholewiak et al., 2018). However, evidence from a study conducted in eastern Australia supports the hypothesis that songs are signals for females. In this study, a significant proportion of singers preferentially joined mother-calf pairs rather than any other group type. Singers associated longer and sang for a significantly greater proportion of time while escorting mother-calf pairs (Smith et al., 2008). Finally, Dunlop and Noad (2016) showed that while males used song to join with females, they did so less when there were other singers and potential

competitors in the area as continuing to sing might be 'risky'; they interpreted this as supporting a dual song function with song being used to court females but with eavesdropping males also using song to potentially assess competitors.

1.4.4. Geographic Variation in Song

Humpback whale songs of individuals in acoustic contact tend to be more similar than geographically separated whales (Cholewiak et al., 2012). However, the scale at which similarity is maintained can be extremely large. Cerchio et al. (2001) compared songs produced in Isla Soccorro, Mexico and in Kauai, Hawaii (4800 km apart) within a breeding season. Whales in the two study sites were singing analogous themes and changes occurred synchronously in a consistent set of variables in both areas within the breeding season. Similar results were observed by Darling and Sousa-Lima (2005) between song from Brazil and Gabon (5500 km apart). This analysis revealed an overall similarity in theme organisation between songs from the two breeding grounds during the same season. However, when songs from Madagascar and Western Australia (~6500 km apart) were compared during the 2006 breeding season the two regions shared only one theme while presenting between four and six themes unique to one or other of the populations, suggesting some degree of connectivity between the two populations (Murray et al., 2012). All these results derive from songs recorded in different breeding grounds; however, in recent years acoustic sampling effort in high latitude areas has increased significantly, resulting in substantial evidence that singing activity is present during the feeding season, even if less predominant than the breeding grounds (Mattila et al., 1987; Stimpert et al., 2012; Vu et al., 2012; Stanistreet et al., 2013; Magnusdottir et al., 2015; Español-Jiménez and van der Schaar, 2018). Song recordings from feeding grounds can be extremely valuable to track the migration pattern of a population. As an example, four song themes recorded in 2009 off eastern Australia were matched to four themes heard in 2010 off Antarctica (area V); furthermore, the same four themes were recorded at the end of 2010 in New Caledonia (Garland et al., 2013a). These observations confirmed historical and photo-identification studies that linked the eastern Australian population with the Antarctic feeding area V (Chittleborough, 1965; Franklin et al., 2012; Constantine et al., 2014). These results also highlighted the potential importance of feeding grounds as key locations for song

transmission between the eastern Australian and the New Caledonian populations (Garland et al., 2013a). In general, the geographical variation in songs suggests a correlation between song similarity and geographical distance. For instance, a study conducted on songs recorded in three study sites across the North Pacific (Philippines, Japan and Hawaii) showed that songs from geographically closer sites were more similar in terms of their phrase composition (Darling et al., 2014). These studies underline also how the understanding of migratory corridors is of key importance in order to evaluate and contextualise song divergence at the ocean basin level.

1.4.5. Cultural Transmission of Humpback Whale Songs

Like males of several bird species (Slater, 1986), humpback whale males in acoustic contact tend to conform to the same themes, resulting in a collective convergence towards the same song type. Moreover, songs are in constant evolution, and individuals keep up with the variations, singing the most updated version of the song (Payne et al., 1983; Payne and Payne, 1985). Songs from different individuals tend to be very similar, and there is also variation between different song cycles from the same individual such that variation is thought to be equivalent within and between individuals (Darling and Sousa-Lima, 2005; Cholewiak et al., 2012). The behavioural or physiological rules behind song evolution are still not completely clear. Cerchio et al. (2001) observed analogous and synchronous variations between Hawaiian and Mexican songs and proposed that some features of songs may undergo changes according to predetermined patterns when cultural transmission is limited. Phrase duration and unit structure may change according to a whale's innate template or a set of learnt rules (Cerchio et al., 2001). However, the most widely accepted theory is that songs evolve gradually and their changes are transmitted via social learning among males. Noad et al. (2000) described another type of song change off eastern Australia, which was more rapid than the song evolutions recorded in previous years. This rapid evolution, termed a 'song revolution', was characterised by a complete replacement of the song sung by the eastern Australian population between 1996/97 by the introduction of a novel song (hereafter referred as 'revolutionary song'), belonging to the western Australian population. The entire replacement of the song by a male population of roughly 1800 individuals (Paterson et al 2001) took less than two years. The song revolution recorded

in eastern Australia between 1996-98 was not an isolated event - Rekdahl (2012) documented three further song revolutions occurring between 2002 and 2010. All of the revolutionary song types originated from songs sung by the western Australian population. These dramatic song replacements suggest that novelty might play a role in song learning and that change of such speed that it could only be culturally driven (Noad et al., 2000). A pivotal study confirmed the conclusions of Noad et al. (2000) by tracking the horizontal cultural transmission of eight song types across multiple populations in the South Pacific over the course of 11 years (Garland et al., 2011). These eight song types all spread eastwards, with four of them crossing the entire region, from eastern Australia to French Polynesia, more than 6000 km apart. The temporal and geographical scale of this song transmission, together with its high fidelity, strongly confirmed the cultural nature of humpback whale song learning (Garland et al., 2011). This study also highlighted the potential importance of migratory corridors and feeding grounds for song transmission and population connectivity (Garland, 2011; Garland et al., 2013a; Garland et al., 2015). This revolutionary mode of song transmission presents a scientific puzzle, and understanding how song learning interactions involving individual whales lead to these events is the core motivation of this thesis.

1.5. Thesis Overview

This thesis focuses on cultural evolution and transmission of humpback whale songs by investigating the individual learning strategies involved in the population level song characteristics observed in the wild. These cultural evolution processes are investigated both theoretically (chapters 2 and 3) and empirically (chapter 4). In chapter 2 I introduce a novel spatially explicit agent-based model that simulates the spatial and acoustic behaviour of humpback whales. This model is used to investigate the individual learning mechanisms behind population song conformity, song evolution and geographical variability. The model architecture is updated with new geographical scenarios and learning biases in chapter 3 to explore in depth the process of song revolution occurring in eastern Australia. In chapter 4 song data collected in 2002 and 2003 is used to empirically measure inter and intra-individual song variability across a pool of 25 singers. The analysis is conducted at different hierarchical levels in different

song types (evolutionary and revolutionary) in order to measure conformity and identify potential individual idiosyncrasies.

In chapter 2 a spatially explicit agent-based model is used to understand the individual learning mechanisms that drive both song conformity and evolution in humpback whale songs. The model simulates the migratory movement patterns of humpback whales, a simple song learning and production method coupled with sound transmission loss, and a variable singing probability during the different phases of the migratory cycle. Initially, a parameter space analysis is carried out in a simple geographical set up to measure how sensitive the emerging song conformity is to the different parameter settings. The model is then extended to include cognitive biases that may be responsible for driving changes in the song, such as a bias towards novel songs, production errors, and the coupling of novel song bias and production errors. All the levels of song convergence and evolution resulting from the different learning biases and geographical scenarios are then compared against each other as well as against real song data recorded in 2002 and 2003 off the coast of eastern Australia.

In chapter 3 the potential individual behavioural rules at the origin of the song revolution events recorded in eastern Australia are investigated by developing further the basic modelling architecture of chapter 2. Here, three distinct geographical scenarios are tested in order to simulate the potential interactions between the western and eastern Australian humpback whale populations. In the first scenario, where sound transmission loss is the only factor influencing song learning, I explore how the interplay between population density, differences in population size and spatial overlap during the feeding season could allow the emergence of song revolutions. In the second and third geographical scenario I introduce and test a new learning bias based on sound transmission loss and individual song memory. Here, the interactions between population density, agents' song memory, bias towards pre-existent song memory, and variable singing probability during the feeding season are explored to understand which parameter settings favour the emergence of song revolutions. Based on the results of the three scenarios tested, I formulate two general hypotheses regarding the potential origins and individual behavioural mechanisms involved in song revolutions.

In the fourth chapter intra- and inter-individual variability in song production is quantified using two key song type examples: the gradually changing evolutionary song sung in eastern Australia in 2002, and the revolutionary song introduced into the same population the following year (2003). Variability is measured at different levels of the song hierarchy, from the sub-phrase to the song cycle. A robust song similarity analysis method, the Levenshtein Distance, is employed to measure variability in sub-phrases and songs produced by 25 distinct singers. Based on the results I formulate hypotheses regarding the potential role of song conformity and individual idiosyncrasies in advertising cognitive fitness to females.

Chapter 2

Using agent-based models to understand the role of individuals in the song evolution of humpback whales (*Megaptera novaeangliae*)

2.1. Abstract

Male humpback whales produce hierarchically structured songs, primarily during the breeding season. These songs gradually change over the course of the breeding season, and are generally population-specific. However, instances have been recorded of more rapid song changes where the song of a population can be replaced by the song of an adjacent population. The mechanisms that drive these changes are not currently understood, and difficulties in tracking individual whales over long migratory routes mean field studies to understand these mechanisms are not feasible. In order to help understand the mechanisms that drive these song changes, I present here a spatially explicit agent-based model inspired by methods used in computer music research. I model the migratory patterns of humpback whales, a simple song learning and production method coupled with sound transmission loss, and how often singing occurs during these migratory cycles. This model is then extended to include cognitive biases that may be responsible for driving changes in the song, such as a bias towards novel song, production errors, and the coupling of novel song bias and production errors. While none of the methods showed population song replacement, the model shows that shared feeding grounds where conspecifics are able to mix provides key opportunities for cultural transmission, and production errors facilitated gradually changing songs. These results point towards other learning biases being necessary in order for population song replacement to occur.

2.2. Introduction

Humpback whales have been intensely studied for more than 40 years, attracting different generations of researchers due to the complex, stereotyped songs produced by males (Payne and McVay, 1971). All over the world, whales in acoustic contact, usually within a breeding population, tend to conform to the same song display; across time, songs gradually change (evolve) and, generally, the individuals of a population manage to keep up with the changes singing the most updated version of the display (Winn and Winn, 1978; Payne et al., 1983; Payne and Payne, 1985). In certain cases, this highly conformist system changes abruptly when a new song is introduced presumably by a few individuals, leading the whole population to quickly abandon the old song and conform to the novel display (Noad et al., 2000; Garland et al., 2011). While these population-level events have been recorded and studied extensively, the individual mechanisms that allow humpback whales to maintain a high degree of conformity over continuously evolving songs, as well as switch quickly to a novel song when this is introduced in the population, remain unclear. It is not currently feasible to track individual whales over timescales relevant to breeding seasons while also monitoring their acoustic interactions and song production. However the use of agent-based models, where individual agent behaviour can be controlled and the population level outcomes can be compared to empirical observations, offers one way toward generating hypotheses about song learning at the individual level. Therefore, I present here a theoretical investigation based on agent-based modelling that aims to identify individual learning strategies that might produce the population level song characteristics observed in humpback whales.

Theoretical studies that focus on conformity and cultural evolution across different taxa are extremely useful in providing new insights and contributing to the ongoing debate relative to the selective forces behind cultural evolutionary processes. Moreover, investigating vocal convergence can be extremely helpful in order to understand social structures, group cohesion, group identity and affiliation (Tyack, 2008) as well as social complexity (Freeberg et al., 2012). The presence of song conformity within humpback whale populations is not an isolated instance across animal cultural evolution, but rather a very peculiar example of a more general process

of group vocal convergence common to multiple taxa (Tyack, 2008). Birds represent a well-studied group in particular for the investigation of cultural evolution and transmission of acoustic displays such as songs. Birdsong dialects have a long history of study (Marler and Tamura, 1964) and the role of vocal learning in the development of song variation has been investigated in several species (Catchpole and Slater, 2008b). Moreover, vocal plasticity affects the emergence of within-group song and call convergence even when the groups are artificially assembled from unrelated birds of different flocks (Mammen and Nowicki, 1981; Nowicki, 1989; Baptista and Schuchmann, 1990; Farabaugh et al., 1994; Hile and Striedter, 2000). Among mammals, female greater speared-nosed bats (*Phyllostomus hastatus*) modify their calls as a result of group composition changes, achieving an increased similarity among the new group members (Boughman, 1998). Among marine mammals, killer whales (*Orcinus orca*) show stable vocal traditions over a period of 25 years (Ford, 1991), and captive studies suggest that individual killer whales can learn from their conspecifics (Bain, 1986; Crance et al., 2014). Sperm whale (*Physeter macrocephalus*) population structure appears to be characterised by vocal 'clans' (Rendell and Whitehead, 2003; Gero et al., 2016a), that present strong conformity to a shared vocal pattern (Gero et al., 2016b) which remains stable over decades (Rendell and Whitehead, 2005).

Humpback whales represent an extreme example of vocal conformity due to the large geographical and demographic scales at which this phenomenon occurs and the high fidelity with which vocal patterns are transmitted. Male humpback whales produce long**,** complex, stereotyped, and hierarchically organised sound sequences, 'songs', first described by Payne and McVay (1971). Songs consist of individual sound 'units' grouped into a 'phrase' – a series of phrase repetitions constitutes a 'theme', and a 'song' is a cycling sequence of themes. The production of songs is exclusive to males (Winn and Winn, 1978; Tyack, 1981; Glockner, 1983), and this strongly indicates that song is a sexually selected trait which plays an important role in mating behaviour (Herman, 2016). Males within a population usually conform acoustically to a common song (Winn and Winn, 1978). Two species of birds present a similar type of male-only vocal convergence at the colony level: village indigobirds (*Vidua chalybeata*) (Payne, 1985) and yellow-rumped caciques (*Cacicus c. cela*) (Feekes, 1982), but with important differences compared to humpback song. Within a neighbourhood, indigobird males

tend to imitate singers with high mating success and males tend to retain their songs from one year to the next, with only minor changes to the song structure (Payne, 1985). Conversely, the content of humpback whale songs changes gradually and continuously over time (termed 'song evolution') (Payne et al., 1983) as units and/or themes are added, modified or deleted (Payne et al., 1983; Payne and Payne, 1985; Cerchio et al., 2001). However, Noad et al. (2000) described another type of song change off eastern Australia, termed a 'song revolution', characterised by a complete replacement of the song sung by the eastern Australian population between 1996 and 1998 by the introduction of a novel song, belonging to the western Australian population. This dramatic song replacement was a learning phenomenon of such speed it could only be explained by cultural transmission. Further studies have described the eastward spread of different song types across contiguous populations breeding in the western and central South Pacific (Garland et al., 2011), highlighting the potential importance of migratory corridors and feeding grounds for song transmission and population connectivity (Garland, 2011; Garland et al., 2013a; Garland et al., 2015). All humpback whale populations, excluding the one found in the Arabian Sea, migrate annually between high-latitude feeding grounds and low latitude breeding grounds (Clapham, 2000) and singing occurs predominantly, but not exclusively, during the migration and the breeding season (Payne and McVay, 1971; Cato et al., 2001; Noad and Cato, 2007; Stimpert et al., 2012; Vu et al., 2012; Garland et al., 2013a).

The complexity and the dynamism (song evolution vs. revolution) of the acoustic behaviour of humpback whales, coupled with the geographical scale at which whales move and transmit their songs, make the experimental study of this species extremely challenging. Moreover, due to the logistics of fieldwork – and the impossibility of captive studies – recordings of individuals are typically applicable to only a single point in time. This means that there is very little information on song changes in individuals, and acoustic studies have mainly focused on song similarity within and between populations. Due to these difficulties, the mechanisms that drive whales to dramatically change their song repertoires during song revolutions while paradoxically retaining song convergence in between such events are yet to be understood. Similarly, the differing patterns observed in the North Pacific, where breeding populations separated by thousands of kilometres sing the same song (Cerchio

et al., 2001) or similar versions of it (Darling et al., 2014), and the South Pacific, where periodic 'revolutionary' changes typically cause breeding populations to sing different songs at any given time (Noad et al., 2000; Garland et al., 2011), are unexplained. The first step towards solving this conundrum is to understand how individual humpback whales learn from each other and how they are able to maintain population-wide song conformity while songs are showing continuous cultural evolution, but the challenges of following individual humpback whales for more than a few hours at a time are immense. Therefore, I used an agent-based modelling approach to study the humpback whale song system using a bottom-up approach, programming behaviour at the individual level and observing outcomes at the population level.

Individual based models have shown how the accumulation of copying errors and the introduction of new song types through population turnover could lead to the development of local dialects (Goodfellow and Slater, 1986; Slater, 1986; Williams and Slater, 1990). Subsequent studies have highlighted how aggression towards non-conformers can evolve, and potentially lead to population convergence in song (Lachlan et al., 2004). Other spatially explicit modelling studies looked at the factors affecting song divergence between contiguous populations of songbirds under a variety of vocal learning modes (pre and post-dispersal learning, song-based mating preferences, genetic and cultural mutations among others), finding that intra-sexual selection – song matching between neighbours – and female song preferences towards the songs of their population were the main factors driving the formation and maintenance of dialects (Ellers and Slabbekoorn, 2003; Rowell and Servedio, 2012). More recently, agent-based models have been developed to test the roles of conformity, innovation, and random errors (as well as other learning strategies) in the emergence of dialects in sperm and killer whales (Cantor et al., 2015; Filatova and Miller, 2015). While none of these models incorporate song that approaches the complexity of those produced by humpbacks, agent-based models have, however, been successfully used in music research to create autonomous composition systems in which agents construct their individual song repertoire through their acoustic interaction with other agents (Miranda et al., 2010), as well as investigating the role of novelty in mate selection (Todd and Werner, 1999). Agent-based modelling has found significant application in linguistics, where researchers have used it to show that unidirectional vertical cultural transmission

may be a driving factor in the emergence of structure in language (Kirby, 2001) and has also been used to explain how vowel systems change over time (de Boer, 2002). Finally, Kirke et al. (2011) used agent-based modelling to produce a live musical interaction between simplified versions of humpback whale songs and a saxophone played by a musician. While biologically this did not provide new insight, it showed that these kinds of models could be adapted to the kinds of questions outlined here and hence directly inspired the present study.

The modelling approach presented here aims to simulate both the movement and acoustic behaviour of individual humpback whales. Since humpback whale migratory behaviour is of potentially key importance for the occurrence of inter-population song transmission (Garland et al., 2011), intra-population song conformity (Winn and Winn, 1978) and song revolution events (Noad et al., 2000), these models needed to be spatially explicit. A model that aims to reproduce a natural system in its entirety will likely fail, especially in a behaviourally complex system such as humpback whale populations. However, a bottom-up modelling approach informed by data, and incorporating the salient characteristics of the acoustic and movement behaviour of humpback whales, could still be useful to capture the emergent properties of this system, and to produce testable hypothesis for future field experiments. Using four different modelling scenarios developed from a single agent-based architecture I investigate: (1) the role of sound transmission loss and migratory movement in song conformity, (2) the effect of novelty on an individual's song learning process as well as its influence at the population level, (3) if song production errors may be an important factor in song evolution, and (4) which scenarios produce population level characteristics comparable to the ones observed in the wild.

2.3. Materials and Methods

2.3.1. Model Design

In order to explain the design of the model, here I describe the behaviours of a single agent in detail. Behaviours are divided into three categories: (1) movement rules, (2) song production rules, and (3) song learning rules. At every cycle of the model,

movement, song production, and song learning are carried out sequentially: an agent first moves, then, with a given probability, produces a song, and finally listens to, and potentially learns from, songs produced by other agents (Figure 2.1). A single model iteration (*i*) ends when every agent in the population has carried out these actions. Since only male humpbacks have been observed singing (Winn and Winn, 1978; Tyack, 1981; Glockner, 1983), all agents in the models are considered to be male, and the role of female choice is not investigated here. All models were created in Python using the SciPy package, and based on the design presented in Kirke et al. (2015).

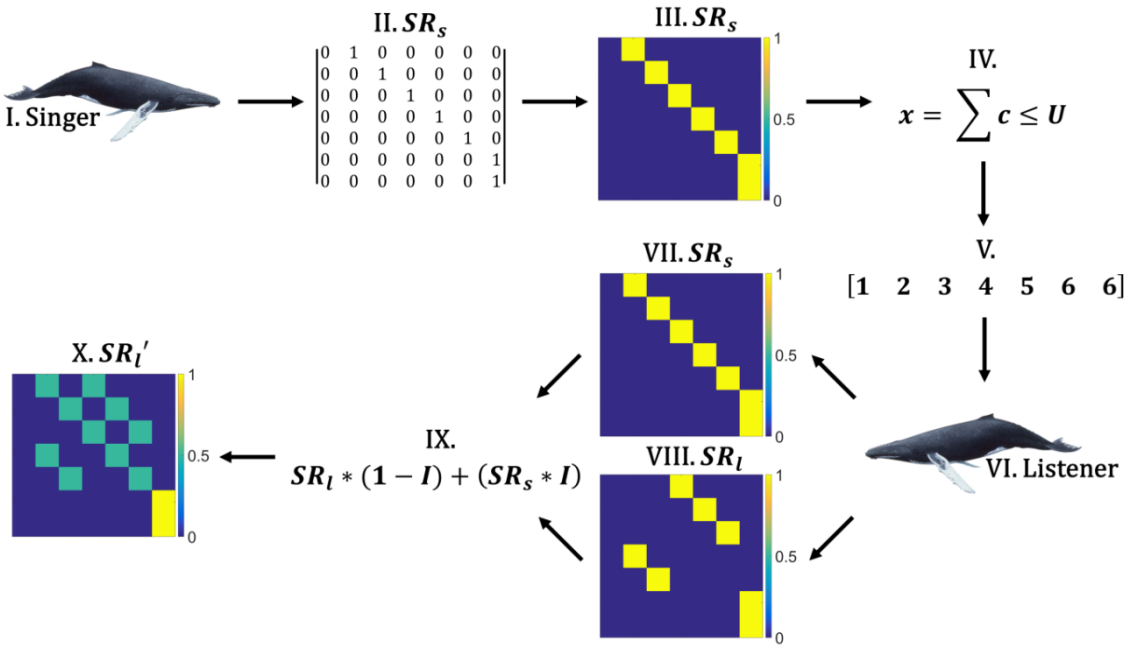


Figure 2.1. Flow diagram of the process of song production and learning. Each singer agent (I) possesses a numeric song representation, SR (II), for visual purposes I represent this with a coloured matrix (III) in which different colours indicate different transition probabilities. The singer agent samples its SR using the equation at (IV), where *x* is the output theme, *c* is the cumulative summation of the probability vector (the row of the transition matrix I is currently sampling from), and *U* is a uniformly distributed random number between 0 and 1, to produce a song sequence (V). The listener agent receives the song sequence (VI), estimates a SR from the song sequence (VII) and compares it to its own SR (VIII) using the weighted average equation (IX), where *I* is the received song salience. Finally, the listener agent updates its own SR completing the learning process (X). (Whale drawing courtesy of Larry Foster).

2.3.2. Movement Rules

In the model, agents exist on a two-dimensional Cartesian plane. In order to simulate the migratory movements of humpback whales at the ocean basin scale, the agents move both within and between a common feeding ground and two geographically distinct breeding grounds (each representing a distinct breeding population). During the feeding season, agents move across the feeding ground using a standard random walk. At the end of the feeding season they simultaneously start their migrations towards their respective breeding grounds (in the two breeding grounds' case, half the agents are assigned to each ground for the entire model experiment). At the end of the breeding season the agents will return to the common feeding ground. Although time is not explicit in the model, the ratio between the numbers of iterations is set to mimic the relative duration of the different seasons, resulting in a migratory cycle comprising 12000 iterations, divided into 2000 migration, 4000 breeding, a further 2000 migration back to the feeding grounds, and finally 4000 iterations in the feeding ground. The maximum speed of the agents is constrained so that agents cannot travel any further than a single integer on the Cartesian plane during a single iteration. This does not confine agents to a strict grid. Agents can exist on decimal points of the grid such as 0.5.

Surrounding each individual agent are two zones of influence with respect to movement: a zone of repulsion (ZOR) and a zone of attraction (ZOA). The ZOR is used to maintain a minimum distance among the moving agents. Two agents in each other's ZOR will calculate a new trajectory in order to avoid each other. In the wild, males have been observed both maintaining some minimum distance while singing (Frankel, 1994) as well as inhibiting each other's singing activity when joining together (Darling and Bérubé, 2001; Darling et al., 2012c; Cholewiak et al., 2018). To mimic this behaviour in the model, two agents will temporarily stop singing while being in each other ZORs. The ZOA is used as an acoustic active space, agents will move towards the nearest singing agent within their ZOAs. This behaviour is based on field observations of males' attraction towards nearby singers (Darling et al., 2012c). In the first part of the analysis I conducted a parameter space exploration in which I tested how varying values of ZOR and ZOA might influence agent's song learning (Table 2.1). In the second part

of the analysis I ran all the models with the ZOR and ZOA set to 0.1 and 10 respectively; these values were selected both on the outcome of the parameter space analysis and the song transmission loss characteristics recorded in eastern Australia (Noad, pers. obs.). These movement rules were modified from existing work on animal collective movement and flocking (Couzin et al., 2002; Shiffman, 2012). At each iteration an agent's movement is a combined function of the rules given by these zones and either a random walk, if on breeding or feeding grounds, or a migratory impulse to head toward a given destination if on migration. If an agent is seeking a target - such as breeding/feeding grounds or another agent - noise is added to the agent's trajectory in order to make their movement patterns less linear. The breeding and feeding grounds are defined as circular areas, and once migrating agents arrive within the target area they revert to random walk movement (Shiffman, 2012).

Table 2.1. Parameters used for the parameter space exploration. Note: the 'size' of each circular area mentioned in the table and in the text (BGS, FGS, ZOR, ZOA) refers to the area's radius.

Parameter name	Parameter value
Number of iterations (*i*)	12000
Number of migration cycles	1
Population size	10, 100
Breeding Ground Size (BGS)	50, 500
Feeding Ground Size (FGS)	50, 500
Zone of Repulsion (ZOR)	0.1, 10
Zone of Attraction (ZOA)	0.1, 10, 100
Maximum song length	100 themes
Song Representation (SR) Matrix Size	5 by 5, 50 by 50
Probability of a song production error (P_e)	0.1, 0.01, 0.001
Singing probability depending on iteration number (*i*) (P_s)	i0-i2000 = 0.5 (migration) i2000-i6000= 0.8 (breeding grounds) i6000-i8000 = 0.5 (migration) i8000-i12000 = 0.08 (feeding grounds)

It is important to note that I deliberately designed the distance values to correspond to the Cartesian plane, and the sizes of the feeding grounds, breeding grounds, and zones of influence are inspired by real world ratios rather than distance metrics such as kilometres.

2.3.3. Song Production Rules

Agents in the model are equipped with a first order Markov model, enabled using a first order transition matrix (Figure 2.1, II). Hereafter I will refer to this as a song representation (SR), as it is a numeric representation of a given song structure. In the model, songs are represented by a sequence of integers. Song is modelled at the

theme level, so that each integer corresponds to a potential theme from a humpback whale song (Figure 2.1, V). While it has been shown that a Markov model cannot adequately capture the hierarchical structure of humpback whale songs when they are represented as a long string of units (Suzuki et al., 2006), more recently this method has been used successfully to represent songs at the theme level (Garland et al., 2017a). The model presented here is best understood as representing songs as sequences of themes, while noting that this abstracts out the complexity of phrase structure found in real song. Agents have a given probability, P_s, of singing at each model iteration – this probability varies depending on whether the agent is on a breeding ground ($P_s = 0.8$), a feeding ground ($P_s = 0.08$) or on migration ($P_s = 0.5$), with values chosen based on empirical observations. An agent produces songs by sampling from the SR transition matrix using the equation in Figure 2.1, IV. The output theme, represented here by a number, is then appended to a list (Figure 2.1, V). The output theme also informs the agent which row to sample from next. Agents use this algorithm in a recursive function to generate songs of varying length. This process continues until the row sampling arrives at the last row of the matrix, at which point the song is considered complete and sampling stops. The resultant sequence of themes is then the realised song of that agent for that single model iteration.

2.3.4. Song Learning Rules

As song is an acoustic signal, its decay was modelled as a function of the distance between a singer and receiver. I calculated what I term the intensity, *I*, of a song arriving at a receiver, as $1/\mathrm{d}^2$, where *d* was the Euclidean distance to the singer. When an agent, the listener, hears the song of another agent, the singer, then it will estimate the transition matrix that generated the received song based on the observed theme transitions. The listener will then update its own SR matrix as a function of this estimated transition matrix, the received intensity (*I*), and learning rules as specified in the following four model scenarios.

2.3.4.1. Model 1: Distance-only

Here, learning depends only on intensity, *I*. The listener's new SR transition matrix, SR_l', is given by:

$$SR_l' = SR_l * (1 - I) + (SR_s * I) \qquad \text{(Equation 2.1)}$$

where SR_l is the listener's original transition matrix, and SR_s is the transition matrix that the listener estimates from the realised song sequence produced by a singing agent. Hence, the degree of learning is a function of distance only. This provides a baseline condition – agents learn what they hear and the closer the singer the more they change their own song to match what they are hearing.

2.3.4.2. Model 2: Distance + Novelty bias

One hypothesis in the literature is that novel songs might be more appealing learning targets for males, possibly due to a preference for novelty on the part of females (Noad et al., 2000; Garland et al., 2011). In order to test the role of song novelty in song convergence and evolution, I introduced a novelty bias, for which a metric of novelty was required. Taking inspiration from the work of Todd and Werner (1999), I calculate novelty as the difference between the transitions an agent expects to hear based on its own SR matrix, and the transitions it actually hears. These differences are then summed, and divided by the total number of transitions observed, in order to create α, our novelty value, which is then used to update the listener's SR matrix as follows:

$$SR_l' = SR_l * \big(1 - (I * \alpha)\big) + SR_s * (I * \alpha) \qquad \text{(Equation 2.2)}$$

Figure 2.2 summarises the difference between the learning processes in models 1 & 2.

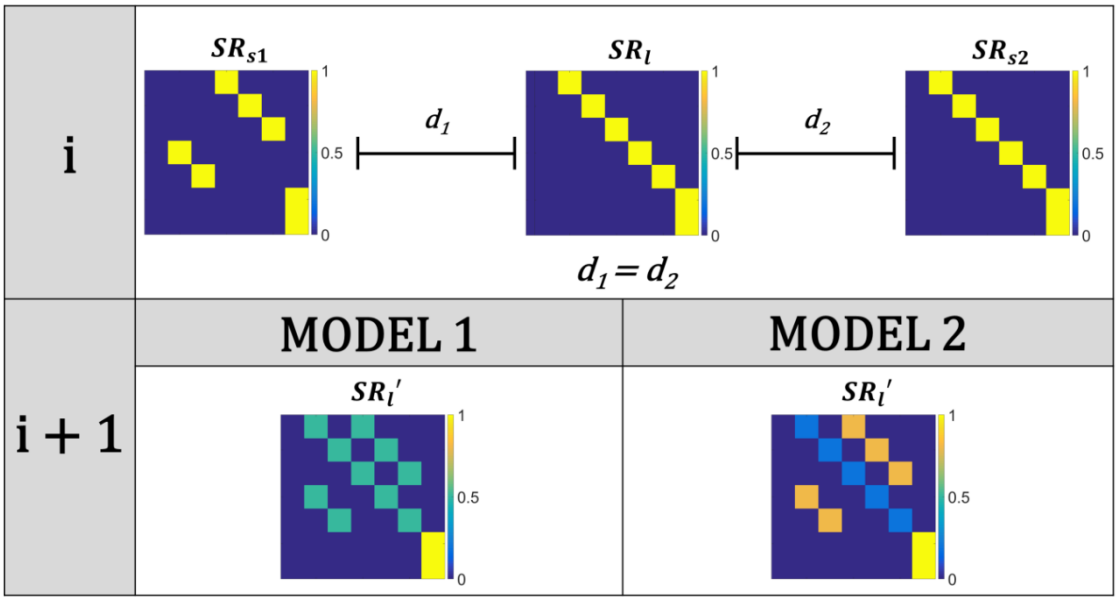


Figure 2.2. Comparison of the learning processes of models 1 & 2 using a common initial spatial scenario. At iteration *i* the listener hears two equidistant singers. Depending which model is implemented, the listener SR at iteration *i*+1 will vary. Using model 1, the transition probabilities of both singer 1 (SR_{s1}) and 2 (SR_{s2}) will be equally represented in the resulting listener's SR. Using model 2, the listener will favour in its resulting SR the more 'unexpected' transitions of singer 1.

2.3.4.3. Model 3: Distance + Weighted-Edit Production Error

Humpback whale songs are likely subject to production errors, as are any other animal vocalisations, and such errors may be important in cultural evolution (Slater, 1986). In order to test the effect of song production errors on song evolution I considered a model with no learning bias but errors in production. A weighted edit approach was used to introduce production errors to the realised theme sequence, using empirical data to weight the probability of a theme being inserted, deleted, or substituted for another.

Based on empirical observations of theme-level song variation in the literature (Payne et al., 1983; Cerchio et al., 2001) a higher probability value (0.8) was given to insertions compared to deletions and substitutions, which were both weighted at 0.1. In order to carry out production errors, the agents first produce a song using their SR matrix, then a production occurs with probability P_e, a parameter of the simulation. If

that probability is achieved against a random number draw, a sequence position is selected at random for editing. Insertion, substitution, or a deletion is selected based on the above probabilities against a random number draw and performed at the selected sequence position. In the case of insertions and substitutions, the new theme is selected at random.

2.3.4.4. Model 4: Distance + Novelty bias + Weighted-Edit Production Error

This scenario represented the most complex hypothesis considered, including distance, novelty bias and production error in order to explore how the combination of all three mechanisms acting on song production and learning would affect the cultural evolution dynamics in the model system.

2.3.5. Model Analysis

Models were analysed in terms of both the changes in the agents' SR matrices, and in the realised song sequences through the model run. Song convergence was measured by calculating the mean SR dissimilarity between pairs of agents within and between breeding populations. The SR dissimilarity between agents *a* and *b* was calculated as $\sum_{i=1}^{n}\sum_{j=1}^{n}|SR_a - SR_b|_{ij}$ where *n* is the size of the SR matrix, and SR_a, SR_b are the SR matrices of agents *a* and *b*, respectively. These values were averaged across pairs of agents in the same breeding population, and pairs of agents in different populations, to give within and between populations mean SR dissimilarity values at each iteration. For each model run (henceforth 'experiment'), I calculated the Δ mean SR dissimilarity as $SR_{i=1} - SR_{i=12000}$ where the mean SR dissimilarity at the end of the experiment ($SR_{i=12000}$) is subtracted to the one at the beginning of the experiment ($SR_{i=1}$) capturing the overall trend of convergence (or divergence) in the experiment. In order to avoid confusing Δ mean SR dissimilarity with the mean SR dissimilarity, the Δ mean SR dissimilarity will be referred to as the ΔMSR for the rest of the text. A ΔMSR of zero means that the agents SR's have not changed at all; the greater the value of ΔMSR the more similar the agents SR's. A negative ΔMSR implies that agents SR's have diverged throughout the model run.

Mean SR dissimilarity therefore measured the degree of vocal conformity of a particular group of agents. Low dissimilarity indicates high convergence while high dissimilarity represents a more variable acoustic system. In order to have an empirical reference, mean SR dissimilarity was calculated based on theme transitions observed from 15 singers' recordings from eastern Australia – in 2002 (7 singers), just before a revolution event, and 2003 (8 singers), just after. I use these empirical values as a reference to interpret how realistic the models' results are, and not as a direct comparison. The realised song sequences produced by the agents were analysed using the Levenshtein distance metric (Garland et al., 2012) to illustrate the variation in songs produced by agents across the modelled populations in a way that is directly comparable to how actual songs are analysed from empirical recordings.

2.3.6. Model Parameters

A parameter space exploration was carried out to evaluate the potential effect of the different parameters (and their interactions) on the degree of conformity within the agent's population (mean SR dissimilarity). A total of 96 modelling experiments were run, and in each experiment a different combination of the parameters indicated in Table 2.1 was used. These model runs consisted of a single population performing a single migration cycle of 12000 iterations between one breeding ground and one feeding ground; song learning occurred according to the distance-only learning rule of model 1 – as I consider this the baseline of the models designed – and agents were all initialized with random SRs. The parameter space for the model was large due to the complexity of the system. The complexity arises from the requirement to allow the creation of specific scenarios that may have a significant impact on cultural transmission in a population of agents.

The results of the parameter space exploration are summarized in Figure 3. In this figure, large ZOR size (10; Figure 2.3, black contour symbols) results in lower ΔMSR across multiple parameter generations when compared to a low ZOR size (0.1; Figure 2.3, grey contour symbols). This implies that large ZOR size results in low levels of song convergence. This is mitigated by increasing the population size, resulting in ΔMSR values going above zero in almost all parameter combinations. This is attributed

to a higher density of agents on the feeding and breeding grounds. The only exception to this overall density related trend is represented by models with a large population size (100), large ZOR (10; Figure 2.3, black contour symbols), medium ZOA (10) and large BGS & FGS (500), in which the ΔMSR decreases just below zero, indicating they have diverged slightly from the beginning of the experiment. A small ZOA (0.1) combined with a small ZOR (0.1; figure 2.3, grey contour symbols), small population size (10) and large breeding and feeding grounds (BGS & FGS = 500) produced the lowest levels of song convergence (lowest ΔMSR in figure 2.3).

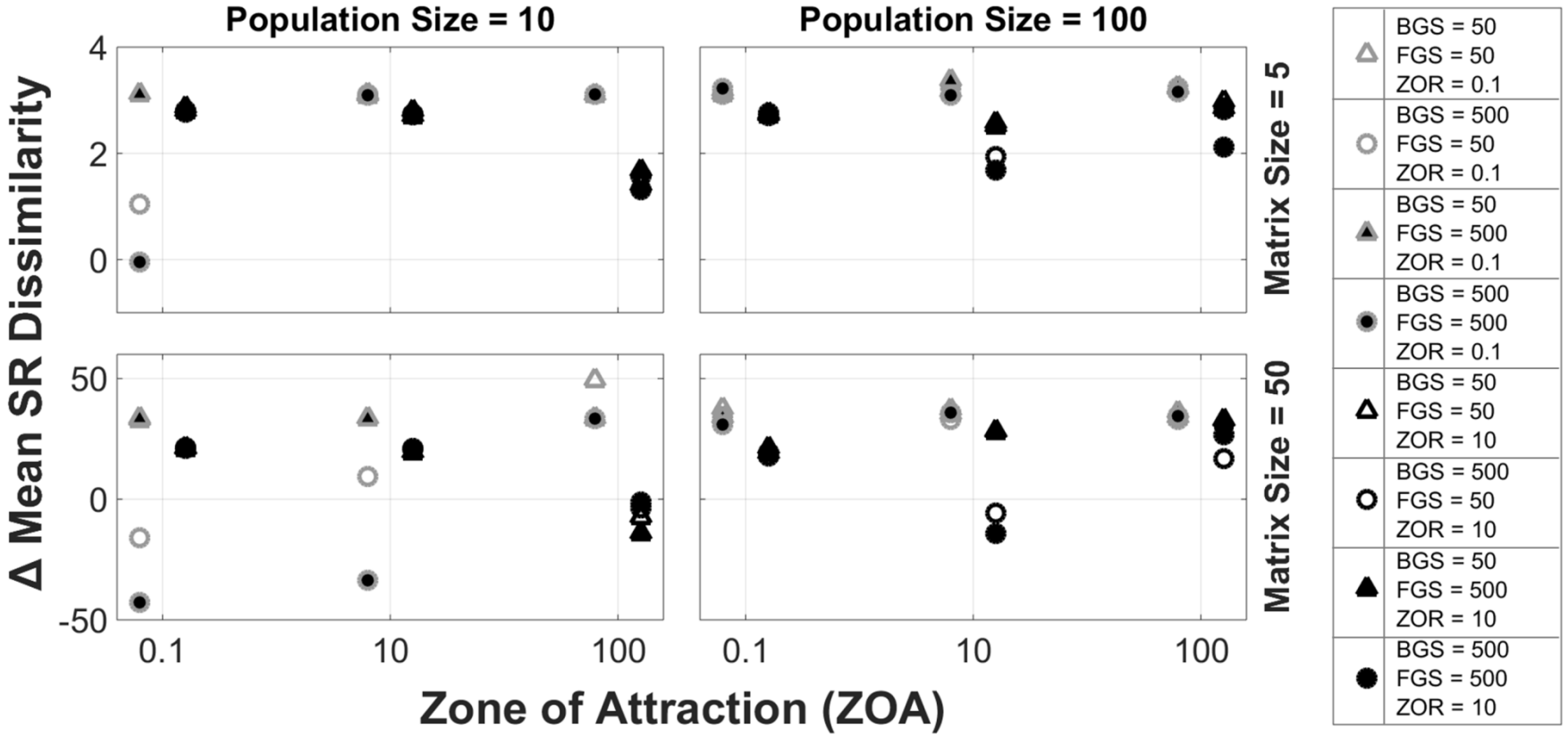


Figure 2.3. Results of the parameter exploration analysis using the distance-only learning bias (model 1). A total of 96 modelling experiments are grouped in four quadrants; each quadrant representing different combinations of matrix size and population size. For each experiment, the Δ mean SR dissimilarity is plotted (y axis) against different zone of attraction (ZOA) sizes (x axis). Grey and black contour symbols represent models with a zone of repulsion of 0.1 and 10 respectively. Each combination of feeding (FGS) and breeding (BGS) ground sizes is represented with a different symbol according to the legend on the right-hand side of the plot.

2.4. Results

Table 2.2. Parameters used in the model experiments presented in this paper. Note: the 'size' of each circular area mentioned in the table and in the text (BGS, FGS, ZOR, ZOA) refers to the area's radius.

Parameter name	Parameter value
Number of iterations (*i*)	24000 12000 for each migration cycle
Number of migration cycles	2
Population size	30 agents total Breeding ground 1: agents 1-15 Breeding ground 2: agents 15-30
Breeding Ground Size (BGS)	100
Feeding Ground Size (FGS)	50, 100, 500
Zone of Repulsion (ZOR)	0.1
Zone of Attraction (ZOA)	10
Maximum song length	100 themes
Song Representation (SR) Matrix Size	11 by 11
Probability of a song production error (P_e)	0.1, 0.01, 0.001
Singing probability depending on iteration number (*i*) (P_s)	i0-i2000 = 0.5 (migration) i2000-i6000= 0.8 (breeding grounds) i6000-i8000 = 0.5 (migration) i8000-i12000 = 0.08 (feeding grounds)

In the model experiments presented here, all the parameters listed in Table 2.2 were fixed with the exception of feeding ground size (FGS), and, when song production errors were introduced the production error rate (P_e). I ran all models (1-4) with three FGS values (50, 100 and 500) and two breeding grounds in order to create three scenarios in which agents belonging to the two separate breeding ground populations either mixed well (FGS50), partially (FGS100), or remained largely separate (FGS500) while on the feeding grounds (Figure 2.4). These scenarios were chosen to explore the

effect of feeding ground size, because acoustic contact on feeding grounds may be an important mechanism to allow song transmission between populations (Garland et al., 2013a). For each of the following feeding ground modelling scenarios, 50 model experiments were run to get a representative view of the model's behaviour.

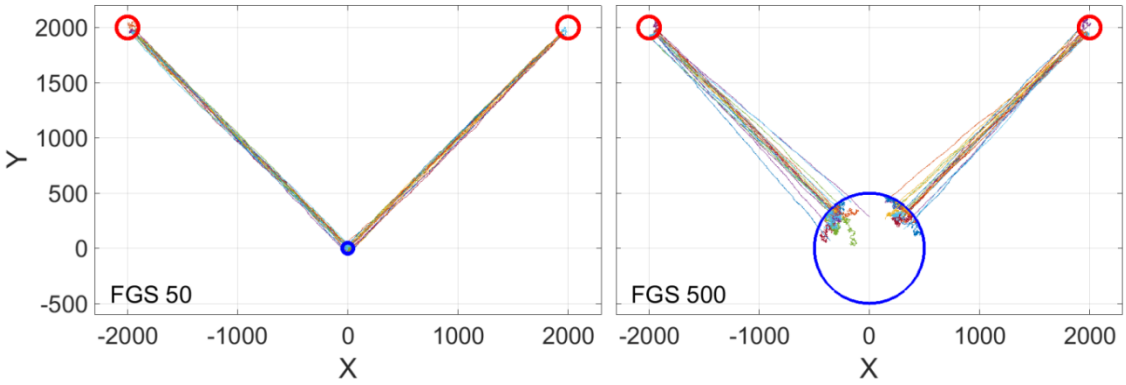


Figure 2.4. Agents' tracks plotted in the two scenarios in which FGS varies from 50 (left panel) to 500 (right panel). Red circles represent the two breeding grounds, blue circles represent feeding grounds.

2.4.1. Model 1: Distance

In all runs the mean within-population SR dissimilarity decreased rapidly during the first breeding season (Figure 2.5, upper panel). With the smallest feeding grounds (FGS=50), once mean SR dissimilarity reached 0 it remained generally low across the remainder of the experiments with the exception of the first feeding season, in which a slight increase was observed due to the mix of agents from the two breeding populations (with different SRs). Mean between-population SR dissimilarity decreased during the first feeding season as agents returned to a small feeding ground until the degree of dissimilarity between the two populations was equal to zero (Figure 2.5, thick orange line, upper panel). A larger feeding ground (FGS = 100) resulted in a more gradual convergence between the two populations during the first feeding season (Figure 2.5, middle panel); however, once the mean SR dissimilarity decreased to 0 it remained low like the previous scenario. If the feeding ground was large enough that the two breeding populations never met (FGS = 500), the mean SR dissimilarity between them remained constant across the two migration cycles (Figure 2.5, lower panel), indicating divergence between populations at the same time as convergence within each. This SR dissimilarity between the two populations was also reflected in the song sequences

produced by the agents (Figure 2.6, i = 6000); although within population song convergence during each breeding season was complete (song dissimilarity = 0), the different breeding ground populations maintained two different songs. Depending how much the two breeding populations mixed during the feeding season, different degrees of song conformity emerged (Figure 2.6 & 2.7, i = 12000). Generally, song sequences produced in all scenarios using model 1 were short. This was due to the agents' convergence on sparse SR matrices with transition probabilities made of 0s and 1s (Appendix 2, Figure A2.1). If two breeding populations have limited contact during the feeding season and/or migration their songs will evolve independently – and likely diverge. However, if the two breeding populations mix enough across a common feeding ground, their original songs will be much similar (or exactly the same) at the end of the feeding season/migration (Cerchio et al., 2001; Darling et al., 2014).

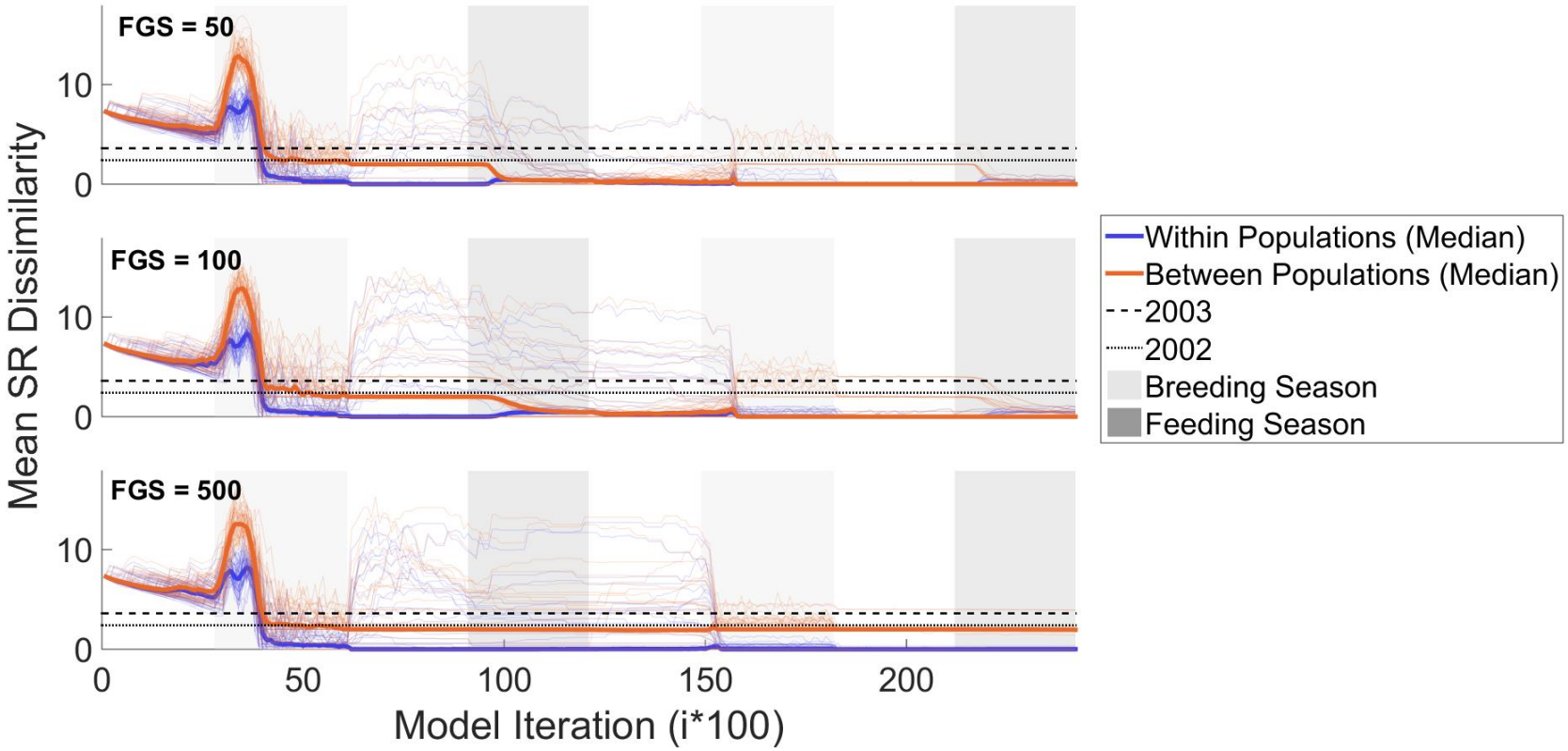


Figure 2.5. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 1. The upper panel shows the results for feeding ground size (FGS) = 50, the middle panel shows the results for FGS = 100 while the bottom panel shows the results for FGS = 500. The blue and orange colored lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is shown with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines are the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

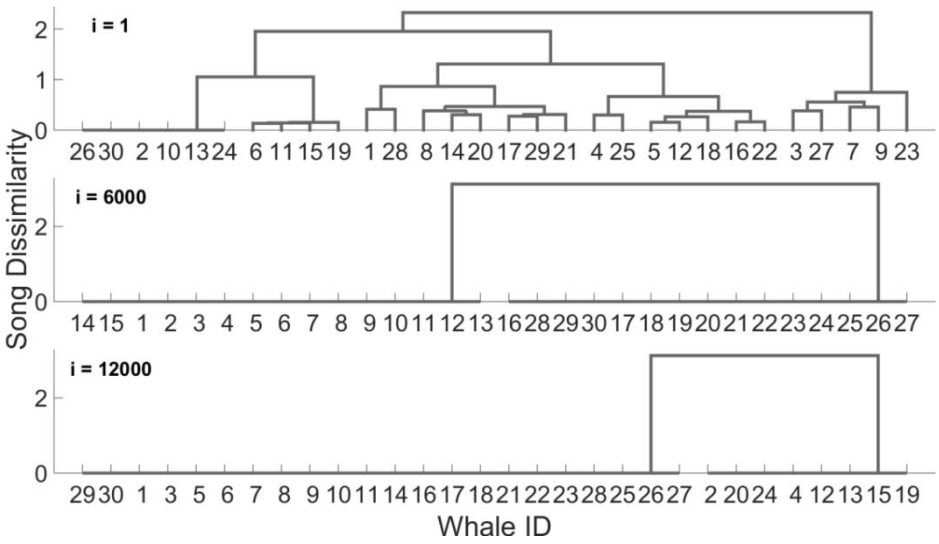


Figure 2.6. Song dissimilarities measured using the Levenshtein distance for model 1. Shows song dissimilarities at the beginning of the experiment (i = 1), the end of the breeding season (i = 6000) and at the end of the feeding season (i = 12000). Agents 1-15 belonged to one breeding population, and 16-30 to the second. Here, FGS = 50.

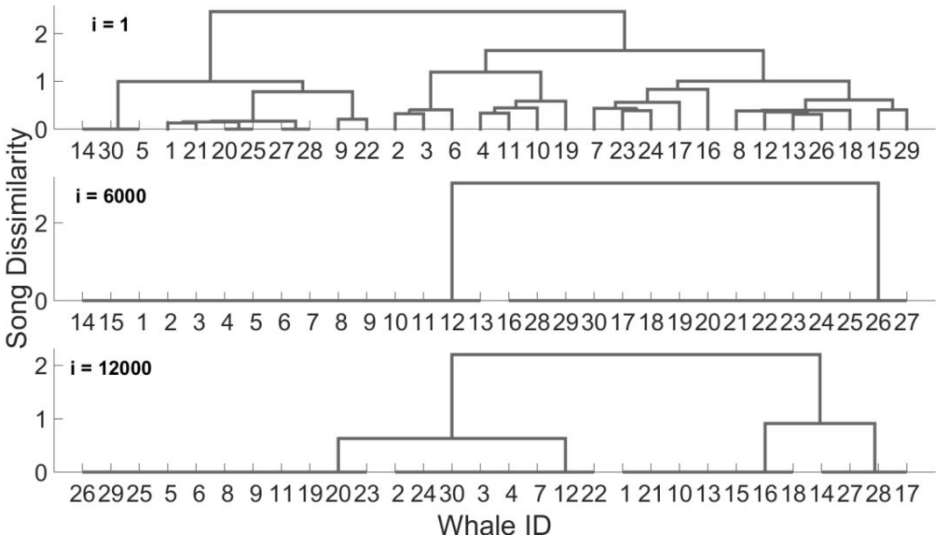


Figure 2.7. Song dissimilarities measured using the Levenshtein distance for model 1. Shows song dissimilarities at the beginning of the experiment (i = 1), the end of the breeding season (i = 6000) and at the end of the feeding season (i = 12000). Agents 1-15 belonged to one breeding population, and 16-30 to the second. Here, FGS = 100.

2.4.2. Model 2: Distance + Novelty bias

When novelty bias was added to song learning, the mean SR dissimilarity generally increased both within and between populations during model runs. The within-population mean SR dissimilarity showed a steady decrease during the first migration cycle following a sudden increase during the second breeding season (Figure 2.8). This increase in dissimilarity was steeper when using a small feeding ground (FGS = 50; Figure 2.8, upper panel) compared to a larger feeding ground (FGS = 500, Figure 2.8, lower panel). Moreover, with larger feeding grounds (FGS = 100 & 500; Figure 2.8, middle & lower panel), the between-population mean SR dissimilarity generally increased across all the experiments toward the end of the simulations. Although the general pattern of mean SR dissimilarity fluctuation was completely different than model 1, divergence between the two breeding populations still emerged.

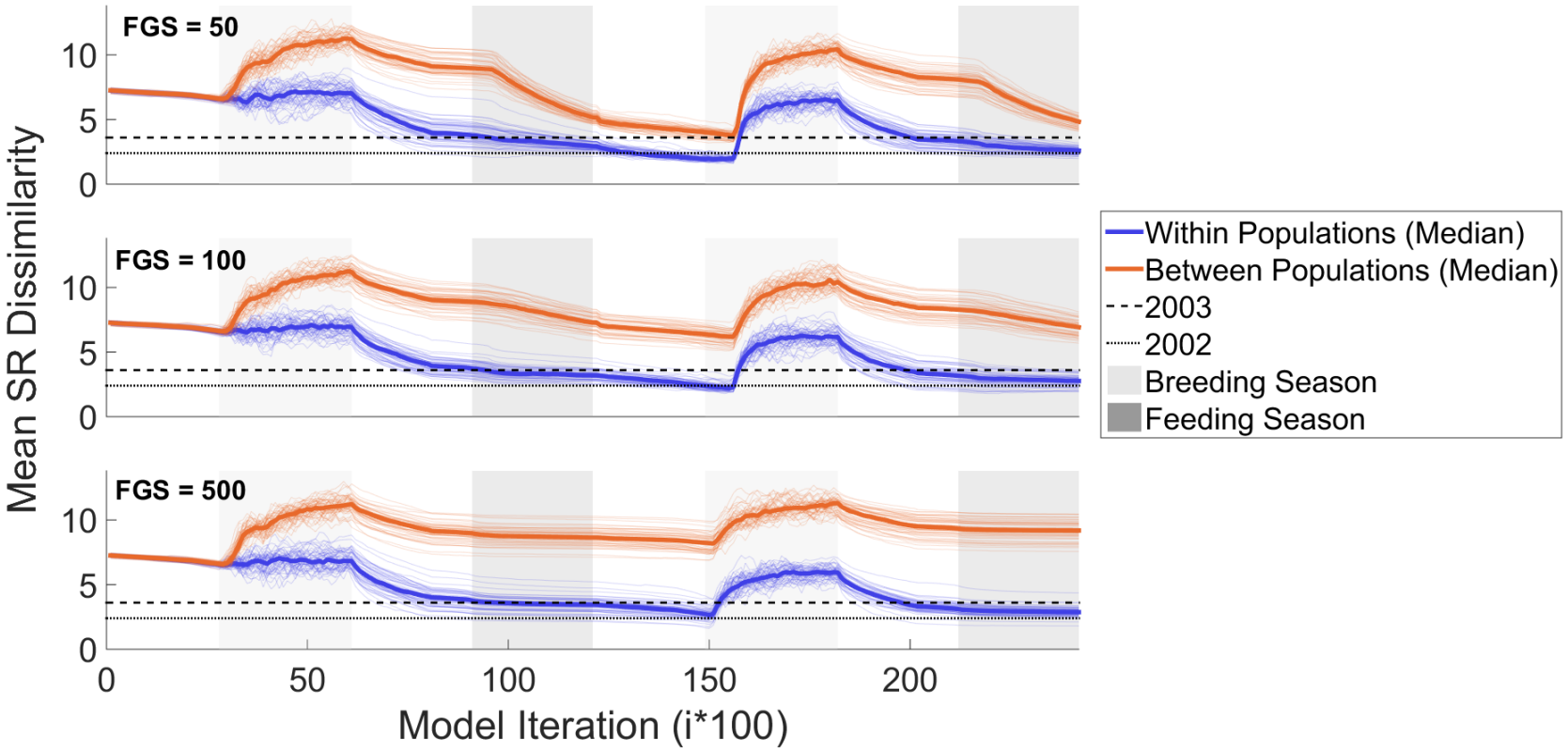


Figure 2.8. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 2. The upper panel shows the results for FGS = 50, the middle panel shows results for FGS = 100 while the bottom panel shows the results for FGS = 500. The blue and orange colored lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is shown with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines are the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

The geographical clustering in songs observed in model 1 was absent when novelty bias was present. The introduction of the novelty algorithm also produced more variable and longer songs compared to model 1 (Figure 2.9); this was due to the fact that SR matrices showed lower and more uniform transition probabilities across themes compared to model 1, leading to a more variable song output (Appendix 2, Figure A2.2).

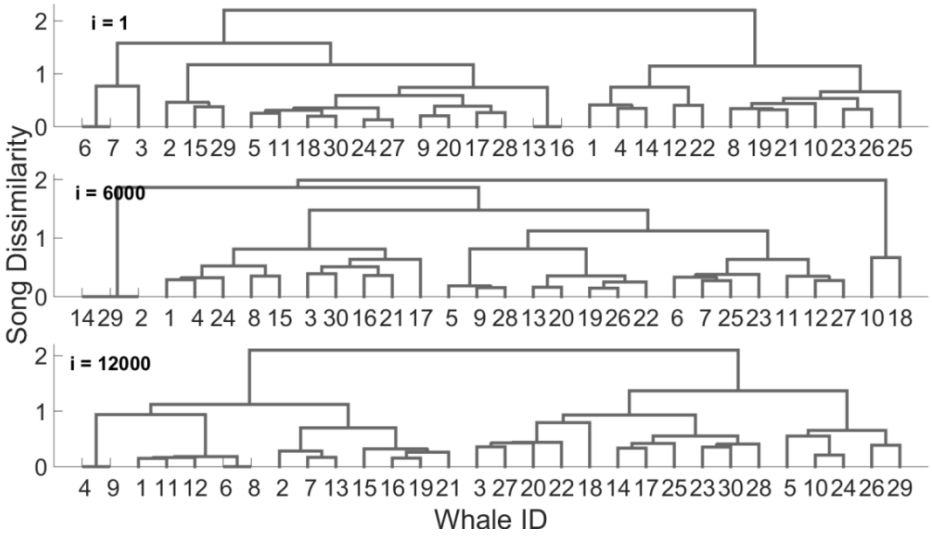


Figure 2.9. Song dissimilarities measured using the Levenshtein distance at the beginning of the experiment (i = 1), and the end of the breeding season (i = 6000) and at the end of the feeding season (i = 12000). Agents 1-15 belonged to one breeding population, and 16-30 to the second. Here, FGS = 100.

2.4.3. Model 3: Distance + Production error

In this scenario the distance algorithm from model 1 was coupled with weighted-edit production errors. Although these models were run with the usual three feeding ground sizes (FGS = 50, 100 and 500), I present here only the results relative to FGS = 50 with P_e = 0.001, 0.01 and 0.1 (Figure 2.10) in order to simplify the presentation of results under the three different edit probabilities. The full results of experiments with FGS = 100 and 500 can be found in Appendix 2 (Figure A2.3 & A2.4), but to summarise, small feeding grounds led to partial (but never complete) song convergence during the feeding season, while larger feeding grounds led to more song divergence between populations, across all production error rates.

The introduction of song production errors triggered more abrupt fluctuations in the mean SR dissimilarity compared to previous results (Figure 2.10). Despite different error probabilities, during each feeding season any divergence accumulated between the two populations during the breeding season disappeared: within- and between-population mean SR dissimilarity reached equal levels with all three edit probabilities. The lowest edit probability (P_e = 0.001) still allows complete convergence (within population median SR dissimilarity reaching 0) during the first and second breeding seasons (Figure 2.10, upper panel), similar to the outcome in model 1. Higher error probabilities (P_e = 0.01 & 0.1; Figure 2.10, middle & lower panel) increased the overall mean SR dissimilarity levels across the entire experiment. The introduction of error probabilities is also visible on the individual SRs, which show between-population divergence as well as more variable transition probabilities compared to model 1 (Appendix 2, Figure A2.5). To test whether this model scenario gave a genuinely different outcome, as opposed to simply slowing down the trends seen in model 1, I ran a model for 10 migration cycles (FGS=50, P_e =0.001), and confirmed that production errors kept the populations from achieving complete within-population convergence (mean SR dissimilarity = 0) over these timescales (Appendix 2, Figure A2.6). This model is important as it shows that simple production errors may be one of the mechanisms driving song evolution.

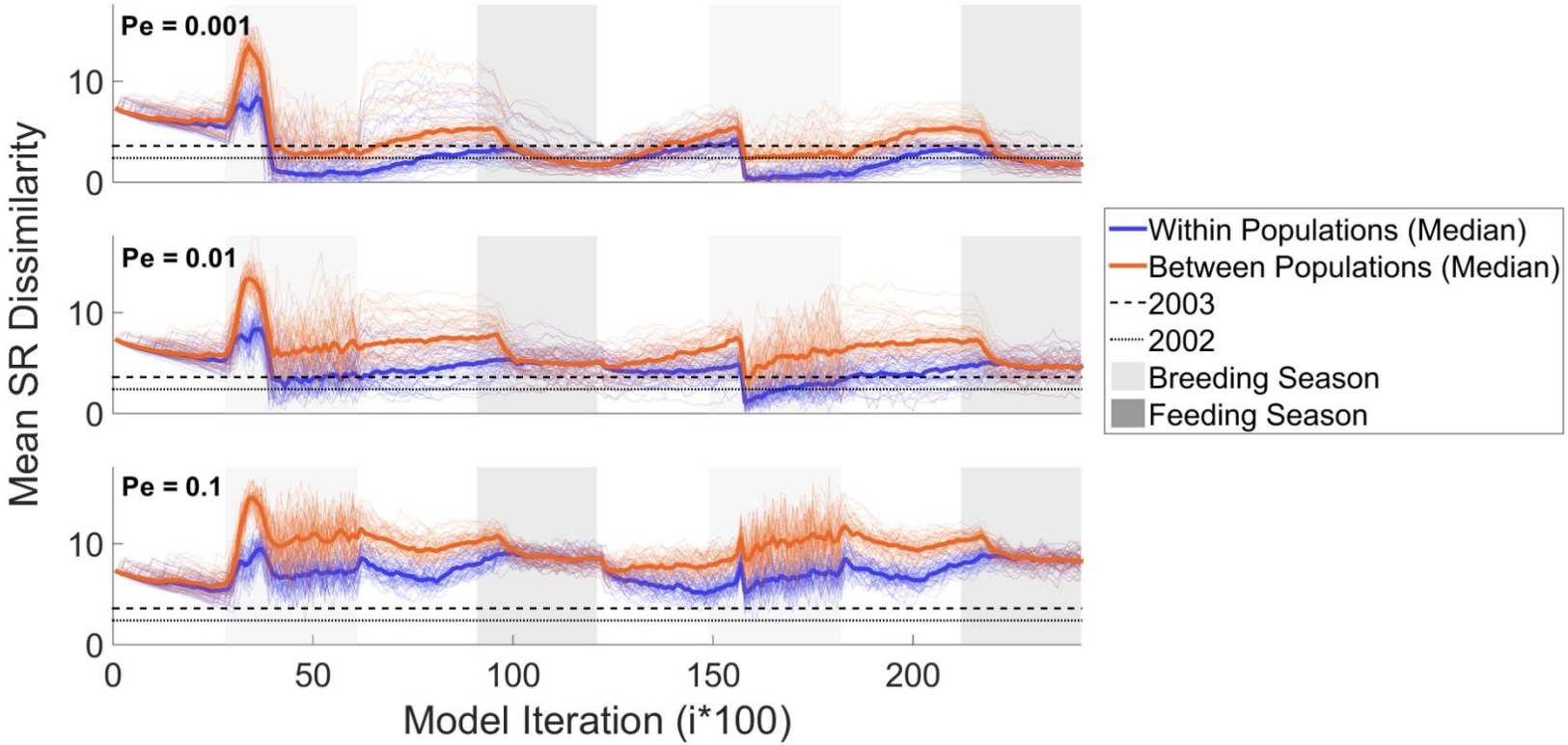


Figure 2.10. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 3. The upper panel shows the results for FGS = 50, P_e = 0.001, the middle panel shows the results for FGS = 50, P_e = 0.01 while the bottom panel shows the results for FGS = 50 and P_e = 0.1. The blue and orange colored lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is showed with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

2.4.4. Model 4: Distance + Novelty bias + Production error

In model 4, the design of model 2 was coupled with the weighted-edits algorithm to test how song production errors might alter the effect of novelty bias on the cultural evolution of song. Similarly to model 3, only results from the experiment with a small feeding ground (FGS=50, P_e = 0.001, 0.01 and 0.1) are presented here (experiments with FGS = 100 & 500 are shown in Appendix 2, Figures A2.7 & A2.8). The introduction of song production error did not qualitatively change the impact of novelty bias, as the results obtained were similar to those for model 2 (Figures 2.11, c.f. 8). There was a slight increase in mean SR dissimilarity during the first breeding season of the simulations when P_e was 0.001 (Figure 2.11, upper panel) compared to 0.01 (Figure 2.11, middle panel). This increase is even more pronounced when P_e = 0.1 (Figure 2.11, lower panel) The peaks of divergence between the populations encountered during the breeding seasons of model 2 were reproduced in this model, and stabilised around the same values (between 6 and 10), irrespective of the production error probability.

The mean SR dissimilarity trends shown in Figure 2.11 are also consistent when models are run for 10 migration cycles (Appendix 2, Figure A2.9). There is a pronounced cyclical pattern of increasing variation (i.e., increasing dissimilarity) between populations during breeding seasons when populations are segregated, which is then erased by the rapid learning of any new variations by the wider meta-population once they are reunited on the feeding grounds.

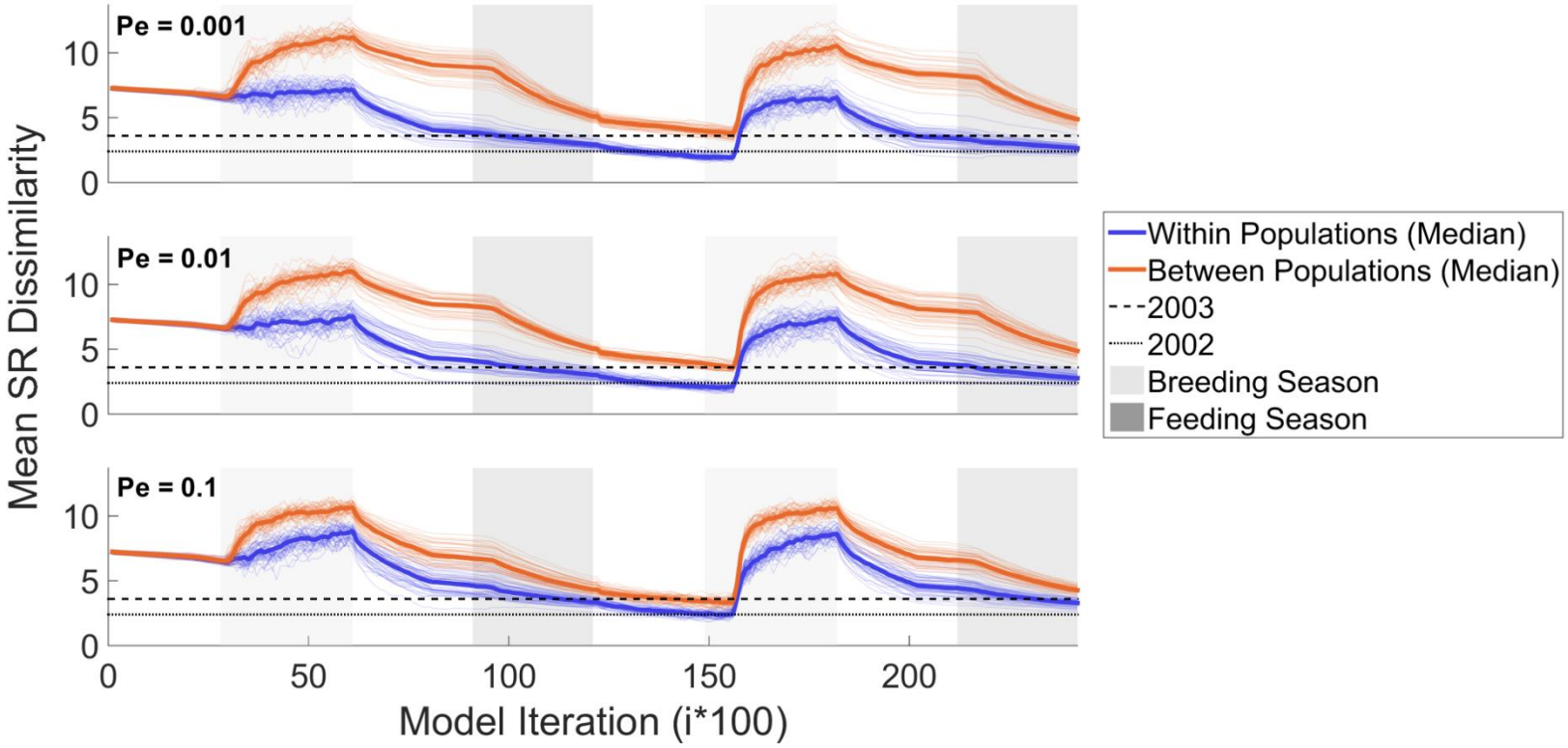


Figure 2.11. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 4. The upper panel shows the results for FGS = 50, P_e = 0.001, the middle panel shows the results for FGS = 50, P_e = 0.01 while the bottom panel shows the results for FGS = 50 and P_e = 0.1. The blue and orange colored lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is showed with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

2.5. Discussion

The spatially explicit agent-based models I analysed broadly show that the spatial relationships between breeding and feeding grounds play an important role in determining song convergence at the population level. However, without some form of variation being introduced, for example by production error, it is very hard to sustain continual evolutionary change. The design of these models was motivated by the desire to understand more thoroughly one of the most striking examples of animal cultural transmission, the patterns of change in humpback whale song. Given the current impossibility of following individual singers in the wild to evaluate how they learn and produce songs, a spatially explicit agent-based model was developed to study how song learning by individuals might produce observed population level patterns.

The first model, in which the only factor controlling song learning was distance from the singer, produced total convergence within breeding populations, an unrealistically extreme result when compared to empirical measures of convergence from the eastern Australian humpback population. Varying the feeding ground size, and thus the extent to which members of the two populations were exposed to each other's song during the feeding season, dramatically altered the extent of between population divergence, even though singing probability was decreased by an order of magnitude between breeding and feeding grounds (0.8 vs 0.08). Small feeding grounds, on which the populations were forced to mix, minimised divergence between populations, while large feeding grounds, where mixing was much rarer, resulted in high divergence between populations. Thus the simplest of the models presented here demonstrates how the spatial arrangement of feeding and breeding grounds can produce quite different cultural evolution outcomes even when the underlying learning mechanisms are the same. This result supports published predictions that feeding grounds and migratory routes are key locations for song transmission (Garland et al., 2011; Garland et al., 2013a). Contrary to observations in the wild, however, the length of songs produced by this model decreased drastically during model runs, and by the end of the model runs agents showed a high degree of song conformity on very short songs. It is not necessarily unrealistic for culturally evolving signals to decrease in length - for example, the range of movement in an invented sign language decreased over multiple

generations of an iterated learning model (Motamedi et al., 2016) - but the decrease in song length in this model is an artefact of the learning algorithm used here. Songs do not evolve within this scenario, because when complete song convergence is reached, the population's song representations become fixed on purely 1/0 transition matrices, unless a new song is introduced (which can happen when two breeding populations with different songs mix on the feeding ground).

Since the simplest model produced unrealistic results, I added a new component to the model to try and understand how a population of agents could show song evolution by the simplest mechanisms possible. Song revolutions recorded in eastern Australia (Noad et al., 2000) indicate that males might be preferentially attracted to novel song introduced by conspecifics from western Australia, so I introduced a novelty bias in song learning. This novelty bias prevented the song fixation observed in model 1; moreover, the mean SR dissimilarity values obtained were on average higher than the real song reference from eastern Australia. However, similar to model 1, large feeding grounds still led to a high degree of song divergence between the populations. This is consistent with what is observed in the South Pacific, where there is clear divergence between breeding populations (Garland et al., 2011). However, other aspects of the results were less realistic. While songs converged (i.e. mean SR dissimilarity decreased) during the feeding season as in model 1 (albeit to a lesser degree), the transition probabilities within agents' song representations decreased such that the produced song sequences became relatively unpredictable (Appendix 2, Figure A2.2). This meant it was no longer possible for any agent in the population to have a 'novel' song with respect to the song representation matrix, as each transition was equally as likely as any other and so there was no expectation to be violated. The increased song variability compared to the distance-only model also meant that while song representations partially converged, agents could produce many different song sequences from those matrices, and so the population did not show true vocal convergence in realised songs. Moreover, this increased song variability did not produce any quantifiable song evolution over time. This was also true for the model that combined novelty bias with production errors (model 4) – the novelty bias had such a strong effect that it negated the effect of the production errors and resulted again in unrealistically variable song sequences. In future work, it will be important to investigate non-linear novelty effects

in the model by allowing agents to have different degrees of novelty preference for songs, and to have increased preferences for songs of intermediate novelty, for example.

Neither model 1 (distance) nor model 2 (distance + novelty bias) produced gradually evolving songs, so were not sufficient to explain observed song variation. To produce continued evolutionary song change after convergence, some mechanism was required to prevent populations 'fixing' on purely 1/0 SR matrices from which no variation could occur. In order to address this I introduced the assumption of song production errors in model 3, based on a weighted-edits algorithm. Informed by humpback whale song literature describing within-population song variation (Payne et al., 1983; Cerchio et al., 2001) I assigned a high probability of theme addition, with theme substitution and deletion being possible, but significantly less likely. The addition of production errors significantly changed the song evolution dynamics in the model. Rather than agents converging on identical transition matrices, they instead maintained a level of dissimilarity which oscillated to varying degrees depending on the probability of production errors. The mean SR dissimilarity calculated at the end of the breeding season in model runs with an error probability of $P_e = 0.01$ matched the empirical range of theme sequence dissimilarities measured from seven and eight singers respectively recorded in 2002 and 2003 off eastern Australia (Figure 2.10, middle panel). In contrast, the most complex model, model 4, showed that novelty bias negated the impact of production errors with respect to cultural evolution, irrespective of their probability, producing results very similar to model 2, and equally unrealistic.

All models are thought experiments that force scientists to abstract out many real-world details, but the models I have presented here, while no different, have been closely informed where possible by empirical observations to help understand how the cultural evolution of humpback whale song might emerge from spatial structure and simple learning and production rules. Modelling for the purpose of studying vocal convergence is not a new idea. It has been used in several fields such as biology, linguistics and music (Goodfellow and Slater, 1986; Slater, 1986; Williams and Slater, 1990; Todd and Werner, 1999; Kirby, 2001; de Boer, 2002; Lachlan et al., 2004; Miranda et al., 2010). While these models study vocal conformity, they do so in strictly defined systems. This simplicity informed my choice of first order Markov models as a

song learning/production substrate in the model, leading to a simple song production and learning system that makes minimal assumptions about the cognitive capabilities of humpback whales whilst also allowing us to incorporate other influential factors that may impact song learning. Moreover, Markov models have been recently and successfully used to describe the structural characteristics of hybrid humpback whale songs at the theme level (Garland et al., 2017a). However, there are a number of problems in using a first order Markov model for song learning and production. Such models will never achieve the level of complexity observed in humpback whale song when songs are examined as a long string of individual units, due to its hierarchal and repetitive structure (Suzuki, Buck, & Tyack, 2006). Despite these shortcomings, the focus here was not on whether or not these models can recreate the syntactical fine-scale structures observed in humpback whale song. Instead, I aimed to model one commonly quantified, reported and representative hierarchical level within the complicated song structure: the sequence of themes comprising a song (Cholewiak et al., 2012; Garland et al., 2017a). By using a simple method of song learning and production, I could easily highlight the effect of environmental factors on the songs of the agents. I consider these Markov models as place-holders that should ultimately be replaced by a way of modelling fine-scale song production that is more closely informed by data from real humpback songs, once they become available (for example, the syntax modelling approach of Jin and Kozhevnikov (2011) shows some promise in this regard). Humpback whale song learning is, of course, a biological system and will be subject to variance in many ways that have not been captured in the current model. For instance, variance among listeners in the rate of song learning in general (Mesoudi et al., 2016), and uptake of novelties in particular could potentially generate asymmetries that may be important in preventing complete song conformity among populations. Nonetheless, the current model produces a number of interesting predictions by modelling the interaction between humpback whales on the breeding ground, how migratory movements influence song learning, how the size of feeding grounds may impact transmission, and how the acoustic loss in transmission of song over distance, among other factors, might influence song learning.

The role of female humpback whales has purposely been excluded from the current implementation of the model, despite their obvious central role in real

populations. This is partly motivated by the need to keep models simple and tractable, but partly also over uncertainty over the role of females in song evolution. Songs are hypothesised to have a role in the mating system of humpback whales, but whether they function in mate attraction and/or to mediate male-male interactions is still debated (Herman, 2016). While it will be important to implement female agents in future modelling architectures, caution is warranted given the lack of understanding of how females may shape song evolution (and revolution). Given the notion that a males' drive for novelty is driven by female choice, one possible implementation comes from evolutionary musicology, where the role of females as 'critics' has been investigated (Todd & Werner, 1999). The novelty algorithm that was implemented in the current study takes direct inspiration from this work, which used a similar algorithm to allow female judges in a population of agents to decide which male agent they will mate with. However, in this model, musical preferences are genetically inherited, and this process is not relevant to what seems to happen within humpback whale populations. Songs are not genetically inherited but rather they are learned horizontally from their conspecifics via cultural transmission (Garland et al., 2011). In future, the introduction of female agents as 'critics' would potentially allow us to generate new theories on how female cognitive preference may influence the genetics of the population.

In summary, by using methods inspired by computational research into the origin of music and music composition, I have developed a multi-agent model that simulates the migratory movements, interactions and singing behaviour of humpback whales. Incorporating a sound transmission loss factor into the model allowed the simulation of song convergence within separate breeding populations and simultaneous divergence between populations. It also highlighted the potential importance of feeding grounds as a key location for song cultural transmission for humpback whale songs, as hypothesised in the empirical literature (Garland et al., 2011; Garland et al., 2013a). A novelty bias was found to increase the overall song dissimilarity among agents, and produced high levels of song divergence when the agents were geographically separated between two breeding grounds. Finally, introducing song production errors resulted in songs that gradually evolved, with song variation approaching that seen in the wild at the end of the breeding season. I was able to mirror the gradual cultural evolution of song, but none of the learning scenarios triggered a process comparable with what it is

observed during a song revolution, indicating that other learning biases might be necessary in order to produce such a dramatic population level song replacement and suggesting an obvious next step in this line of research.

Chapter 3

Agent-based models of humpback whale song revolutions

3.1. Abstract

In this chapter I build upon the results of chapter 2 and explore how individual behavioural rules could lie at the origin of the song revolution events recorded across the South Pacific, in which the song of a population is completely replaced by the introduction of a novel song. The model architecture developed in chapter 2 was modified and updated in order to test three distinct movement scenarios and a new learning bias. In the first movement scenario I explored how the interplay between population density, differences in population size, and proportion of spatial overlap during the feeding season, could allow the emergence of song revolutions. In the second and third movement scenarios I introduced and tested a new learning bias based on song memory. The combination of high population density, high conservatism towards pre-existing song memory, and low singing probability during the feeding season consistently led to the emergence of song revolutions in the simulated populations. Based on the results of the three scenarios tested I formulated a general hypothesis on the potential origins and mechanisms of song revolutions that takes into account factors such as the density of whales on feeding grounds, individual movements between populations, song memory, and individual singer feedback on the degree to which his song matches the acoustic song-scape that surrounds him.

3.2. Introduction

The diffusion of novel behavioural traits across animal communities and the extent to which individuals reach conformity within groups is a topical subject within animal behaviour studies (van Leeuwen and Haun, 2013; Aplin et al., 2015b, a; van Leeuwen et al., 2015). One of the clearest examples of behavioural conformity is represented by the vocal displays of humpback whales. These complex stereotyped sound sequences ('songs'; Payne and McVay, 1971) emitted by males have been recorded in a variety of habitats, ranging from the equators to the poles (Payne and McVay, 1971; Payne et al., 1983; Payne and Payne, 1985; Vu et al., 2012; Garland et al., 2013a). Song structure has been analysed in detail, which has revealed the gradual changes ('song evolution') that occur in them over time (Payne et al., 1983; Payne and Payne, 1985). Almost twenty years ago, a particularly puzzling example of cultural evolution (defined as 'song revolution'; Noad et al., 2000) was reported off eastern Australia. This song revolution was characterised by the complete replacement of the eastern Australian song with a novel song (hereafter referred as 'revolutionary song'), recorded the previous year off Western Australia. The entire replacement of the song within a population of several thousand whales took less than two years. The rapidity, the numbers of individuals involved, and the geographical scale of this cultural process were unprecedented for species other than humans. Building upon the results of the previous chapter, here I use agent-based models to explore the individual learning mechanisms responsible for the emergence of song revolutions. Furthermore, I test different movement and cognitive scenarios to try and understand the key factors behind this cultural process.

The gradual changes that characterise humpback whale songs include the addition, deletion and/or modification of units and/or themes, and this type of song evolution is common, having been recorded in multiple populations across the world (Payne et al., 1983; Payne and Payne, 1985; Cerchio et al., 2001). However, the song revolution described by Noad et al. (2000) between 1996/98 in eastern Australia was quite different. The replacement of the song within a male population of roughly 1800 individuals occurred principally between the southern migrations of 1996 and 1997, since during the northern migration of 1998 all individuals recorded had already

switched to the new revolutionary song. The estimate of 1800 males in the population was based on a total population estimate in 1999 of 3600 ± 440 individuals (Paterson et al., 2001). The song revolution recorded in eastern Australia between 1996-98 was not however an isolated event; between 2002 and 2015 five additional revolutions have been recorded in this population (Rekdahl, 2012; Allen, 2018). All the incoming song types involved in eastern Australian song revolutions were sung in the preceding year by the western Australian population, strongly suggesting some kind of acoustic contact between the populations.

Humpback whale songs are likely to be heard by conspecifics at maximum ranges of 10-15 km (Tyack, 1983; Cato, 1991; Noad et al., 2004; Dunlop et al., 2013), depending on the site-specific acoustic transmission properties. Spatial proximity between whales is therefore necessary in order for a song to be transmitted between individuals and, ultimately, between populations. Consequently, the song transmission occurring between the western and eastern Australian population could originate from individuals moving between populations, carrying their song with them. Under the International Whaling Commission (IWC) assessments the western and eastern Australian populations belong to two distinct breeding stocks: the western Australian population was referred as the southern hemisphere breeding stock D while the eastern Australian population was part of the Oceania populations and identified as breeding stock E1 (IWC, 1998, 2006). Breeding stock D (western Australia) is thought to be one of the largest in the world; the latest abundance estimates gave a population of 33,850 in 2008 (CI = 27,340 - 50,260; Hedley et al., 2011) while the smaller breeding stock E1 (eastern Australia) was estimated at 14,522 whales in 2010 (CI= 12,777 – 16,504; Noad et al., 2011). Between 2000 and 2010 both populations increased at a rate of 10-12% per year, recovering from intense whaling activity (Hedley et al., 2011; Noad et al., 2011; Salgado Kent et al., 2012). It has been known since the whaling era that these two populations migrated towards two distinct feeding areas in the Southern Ocean. The portion of ocean between 70° E and 130° W is called area IV by the IWC (IWC, 1998) and is thought to host breeding stock D while the area between 130° E and 170° W (area V; IWC, 1998) is considered the summer feeding ground of breeding stock E1 (Chittleborough, 1965). Using ‘discovery marks’ (stainless steel tags shot into the animals and later recovered upon the whales’ catch) Chittleborough (1965) confirmed

that whales from breeding stock D and E1 spent their feeding season in distinct areas (IV and V). However, they also reported that among 54 recaptures from animals tagged off Western Australia, two (3.7%) were recaptured within the feeding area boundaries of group E1 (area V). Conversely, out of over 84 recaptures of whales tagged off eastern Australia, 10 (11.9%) were recovered within the feeding area of group D (area IV). In the summer of 1958-59 approximately equal numbers of catches of group D and E1 were reported in an area located towards the eastern edge of group D feeding ground (from 110 E to 130 E). This seemed to indicate that the boundaries between the two feeding areas might be fluid and dependent on fluctuating environmental conditions driving distribution and availability of humpbacks primary food source, the Antarctic krill (*Euphausia superba*) (Murase et al., 2002; Fossette et al., 2014; Weinstein et al., 2017). More recent telemetry and photo recapture studies have confirmed the movements of breeding stocks D and E1 towards the respective feeding grounds of area IV and V (Gales et al., 2010; Franklin et al., 2012; Constantine et al., 2014). However, on a wider geographical scale the increased photo identification sampling efforts, the increased number of satellite tags deployed, and the refinement of genetic techniques, reveal a more complex movement scenario in the southern hemisphere humpback whale populations than previously appreciated. In 2009, eight whales were tagged off east Australia on their southward migration, seven migrated towards the feeding grounds of area V (breeding group E1), while one migrated SW reaching the feeding grounds of area IV (breeding stock D), demonstrating a partial connectivity between the two populations. Different telemetry studies that focused on other breeding stocks reported similar situations in which individuals roamed to feeding areas of other breeding stocks during the feeding season (Robbins et al., 2011; Constantine et al., 2016). In few recorded cases, these feeding ground changes resulted in whales migrating northward towards new breeding grounds, sometimes performing inter-oceanic migrations (Chittleborough, 1965; Pomilla and Rosenbaum, 2005; Stevick et al., 2011; Stevick et al., 2013; Stevick et al., 2016). Recent genetic evidence suggests a low level of genetic differentiation between breeding stock G (West Coast of South America) and E1 (Schmitt et al., 2014) as well as, on a wider geographical scale, low differentiation across the adjacent populations of the South Pacific (excluded stock G; Amaral et al., 2016; Rosenbaum et al., 2017). Thus, current knowledge of movements makes it quite

feasible that song transmission and song revolution could originate from the movement of individuals between geographically adjacent populations either through breeding season movements between breeding grounds and/or, as in the specific case of west and east Australia, through overlap in the feeding grounds.

The song conformity displayed by humpback whale populations suggests a conformist learning bias that drives individuals to copy disproportionately the song sung by the majority of their conspecifics (Henrich, 2004; Whitehead and Rendell, 2015). In light of this potential bias, the question of whether the movement of few migrant individuals towards another population would be sufficient to trigger a song revolution is an open one. Another possibility is that individuals also have an inherent bias towards learning novel/different songs, but this is difficult to reconcile with conformity (Noad et al., 2000; Noad, 2002). Furthermore, a simple novelty bias such as that implemented in the previous chapter presents a problem for driving revolutions because song novelty would be perceived equally by both learning parties. In other words, both the immigrant individuals and the individuals of the receiving population would perceive each other's songs as novel, resulting in a symmetric learning dynamic and song convergence rather than replacement. Studies conducted in the western South Pacific revealed, however, that song transmission and song revolution are highly asymmetric, with songs moving consistently from west to east (Noad et al., 2000; Garland et al., 2011; Rekdahl, 2012). Understanding how conformity and novelty bias might interact to produce song revolutions is therefore a theoretical challenge.

Agent-based models are a valuable tool to explore the effects of novelty bias and learning directionality on the emergence of song revolutions. Results from the previous chapter indicated that when a novelty bias was applied with a symmetric learning dynamic where two populations overlapped on a common feeding ground, no song revolution emerged. One way to break the symmetry of a simple novelty bias is to assume whales have a song memory beyond that represented by their current song. Then, as individuals move from a population to another, they bring with them both their current song and the past learning experiences (i.e. learning interactions with their original population) that led to the formation of their current song. Since an immigrant individual will have a different set of memories than a resident of the receiving

population, an interaction between memory and novelty bias could therefore be the basis for breaking down the symmetry problem. To explore this, here I extend the singing model from the previous chapter by equipping agents with a song memory.

The idea of equipping agents with a memory of acoustic experience is fairly unexplored in agent-based modelling. Memory has to date been implemented in agent-based models mostly in the context of spatial movement and habitat use. Dumont and Hill (2001) showed for example that when sheep are looking for food, the advantages provided by a good spatial memory may vary depending on the complexity of the environment; similarly, in scenarios with highly heterogeneous food abundance, memory was advantageous and lower spatial memory capabilities resulted in agents with lower mean body masses and lower survival rates (Boyer and Walsh, 2010; Esposito et al., 2010). Similarly, Bennett and Tang (2006) investigated the movement of elk (*Cervus elaphus*) in Yellowstone National Park using an agent-based modelling approach. They showed that the interplay between short-term episodic memory and long-term reference memory helped the agents to adapt to changing environmental conditions, locate resources and ultimately, develop migratory behaviours that led to higher survival rates during the winter season. Another study explored how the relationship between agents' memory and habitat persistence (the temporal predictability of resources) influenced population-level movement patterns. In predictable habitats, agents with a short memory tended to be sedentary while a long memory facilitated migratory behaviour (Berbert and Fagan, 2012). There have been very few examples of agent-based models used to investigate language and sound evolution that implemented a vocal or sound memory. Miranda et al. (2003) developed an agent-based model to study the evolution of music in which each agent used a memory to store its song repertoire. A similar approach was used to produce a model to investigate syllable systems in which each agent was equipped with a categorical memory of syllables that was used during an imitation game between the 'speaker' agent and the 'listener' agent (Oudeyer, 2002).

In this chapter then I investigate in depth the song revolution process using the agent-based modelling approach developed and tested in the previous chapter. New movement scenarios are introduced as well as a new learning bias based on song

memory. I evaluate the interaction between parameter space, movement scenarios and learning biases on the emergence of song revolutions, and use these insights to generate new hypotheses on the origin and individual mechanisms at the base of these cultural events. More specifically, this chapter explores three main modelling questions. (1) Could song revolutions emerge autonomously based on the simplest learning bias: sound transmission loss? Here I tested if a combination of population size, migratory movements and population density might trigger the appearance of song revolutions using only sound transmission loss to bias learning toward more spatially proximate sources. (2) Could the emergence of population level song revolutions be influenced by individual song memory? Here I developed the new learning bias based on song memory and tested it against learning algorithms developed in chapter 2. Furthermore, I combined the song memory bias with a new movement scenario that allowed individual agents to interact temporarily with another population during the feeding season. (3) The memory bias was also tested in a different movement scenario that permitted individual agents to pass permanently from one population to another. I tested if this permanent immigration, in combination with the memory bias and different population spatial densities, facilitated the occurrence of song revolutions.

3.3. Materials and Methods

3.3.1. Model Design

The general agent-based model design for the set of experiments presented here did not vary from that presented in the previous chapter. Agent's behaviours were still divided into three categories which governed how the agents (1) moved, (2) produced and (3) learnt songs from their peers. These behaviours were still carried out sequentially within each model's iteration (*i*); each iteration ended when all the agents had carried out these actions. The models were still created in Python using the SciPy package and were based on the original design by Kirke et al. (2015).

3.3.2. Movement Rules and Geographic Scenarios

The basic individual movement rules described in the previous chapter concerning the zones of repulsion and attraction (ZOR and ZOA) were maintained

unchanged. Agents still moved on a two-dimensional Cartesian plane mimicking the migratory behaviour of humpback whales between breeding and feeding ground areas. However, in the set of experiments described here the geographical arrangement of these areas was modified into three distinct movement scenarios (Figure 3.1). These movement scenarios aimed to roughly simulate the western and eastern Australian populations (hereafter referred as populations D and E1 for consistency with IWC, 1998) to study the effects of hypothetical movements between these two populations on the occurrence of song revolutions. In all three movement scenarios the two populations possessed separate breeding grounds (red circles, Figure 3.1). Each population migrated towards its respective feeding areas (feeding area IV and V as per IWC, 1998; blue circles, Figure 3.1); the amount of spatial overlap between the two population during this phase of the modelling experiments depended upon the movement scenario tested.

3.3.2.1. Movement scenario 1: Feeding Ground Overlap

In this scenario some portion of population E1 migrated into feeding area IV, along with all of population D, leading to spatial mixing between the populations (Figure 3.1; Scenario 1). Models run under this scenario were grouped into five sets of experiments depending on the percentage of population E1 heading to area IV - this percentage was set to 50%, 60%, 70%, 80% or 90%, with the remainder of population E1 in each run migrating to the separate feeding area V. This movement scenario was based on the assumption that variations in prey distribution in the Southern Ocean (Murphy et al., 2007) would lead to portions of the E1 breeding stock taking a more south-westerly migration towards area IV, thus interacting with whales from breeding stock D. Although a spatial overlap of this magnitude between these two populations is only hypothetical, individual movements between breeding stock E1 and feeding area IV has been occasionally recorded in the past (Chittleborough, 1965; Gales et al., 2009).

3.3.2.2. Movement scenarios 2: Temporary and 3: Permanent Immigration into Population E1

In movement scenario 2 the two populations, D and E1, remained isolated; each migrating between its respective breeding ground and feeding grounds IV and V respectively (Figure 3.1; Scenario 2). However, during the southward migration of

population D, one agent diverted to feeding area V, thereby mixing with population E1 for the entire duration of the feeding season. At the end of the feeding season the immigrant agent returned to its original breeding ground. During subsequent southward migration all the agents of population D migrated towards feeding area IV without exceptions.

In movement scenario 3 the initial change of feeding ground by one immigrant agent of population D was identical to scenario 2. However, in this scenario, the immigrant agent from population D permanently changed population, and moved northward at the end of the feeding season towards population E1 breeding ground, (Figure 3.1; Scenario 3). During the southward migration of the second migration cycle the immigrant agent migrated to area V along with the other agents of population E1.

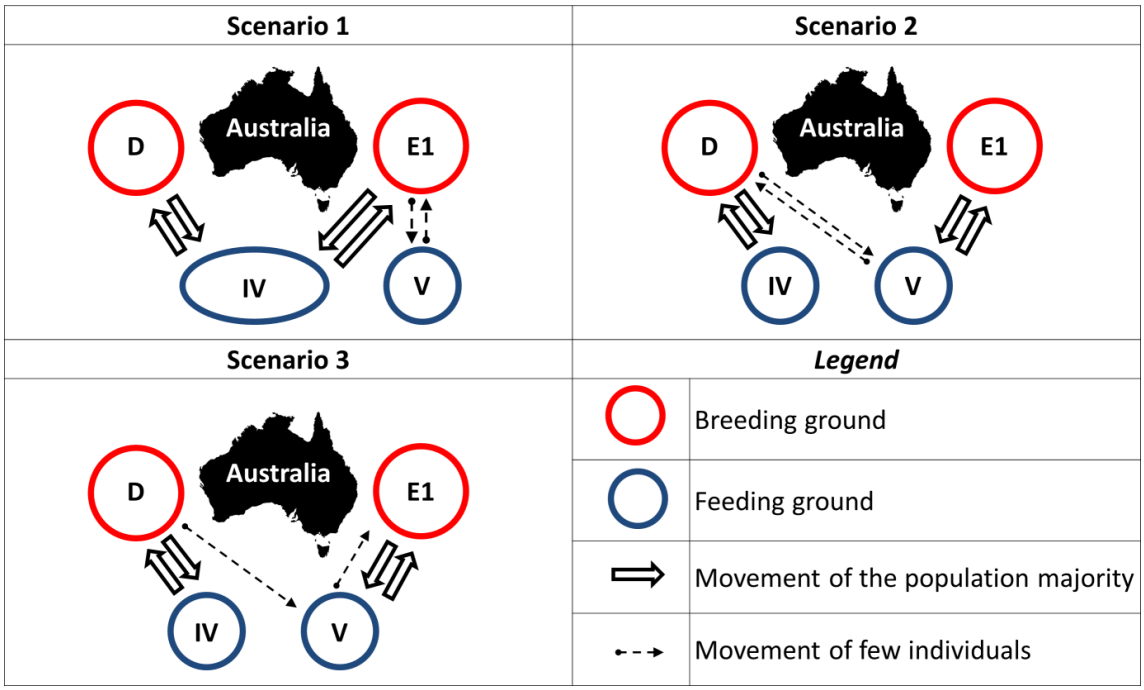


Figure 3.1. Graphical representation the two populations simulated (D, west Australia and E1, east Australia) in the three movement scenarios tested in this chapter.

Scenarios 2 and 3 were based on the assumption that whales from breeding stocks D and E1 were generally migrating to separate feeding areas, which is well supported by the literature (Chittleborough, 1965; Gales et al., 2009; Double et al., 2010; Franklin et al., 2012; Constantine et al., 2014). However, telemetry data and photo identification studies across feeding areas IV-V and across the rest of the South

Pacific confirm occasional anomalous migratory movements by individuals towards adjacent feeding ground areas (Gales et al., 2009; Robbins et al., 2011; Constantine et al., 2016). These occasional movements resulted also in long-term switches of breeding stocks when the immigrant individual migrated northward towards the hosting population's breeding grounds (Kaufman et al., 2011; Stevick et al., 2011; Stevick et al., 2016). Finally, genetic and photo ID evidence corroborates the idea of low interchange between breeding stocks across the South Pacific consistent with these model scenarios (Garrigue et al., 2011a; Garrigue et al., 2011b; Schmitt et al., 2014; Amaral et al., 2016; Steel et al., 2017).

3.3.3. Song Production Rules

In order to maintain comparability between this and chapter 2 results the song production algorithm based on a first order Markov model was not modified. However, instead of initialising the agents with random song representations (SRs) as in chapter 2, the SRs were constructed manually, with the idea of representing two distinct song types. In the previous chapter I used theme transitions from two separate song types recorded off eastern Australia as a reference to better interpret the results. The song of 2002 consisted of 10 themes (giving a 10x10 SR matrix) while the song that was introduced by the song revolution the following year (2003) consisted in only 7 themes (7x7 SR). I wanted to roughly retain these SR sizes, but the model architecture did not allow the assignment of different sized SRs to agents. Therefore I combined the SR sizes from 2002 and 2003 into one single SR sized 17 by 17 (Figure 3.2).

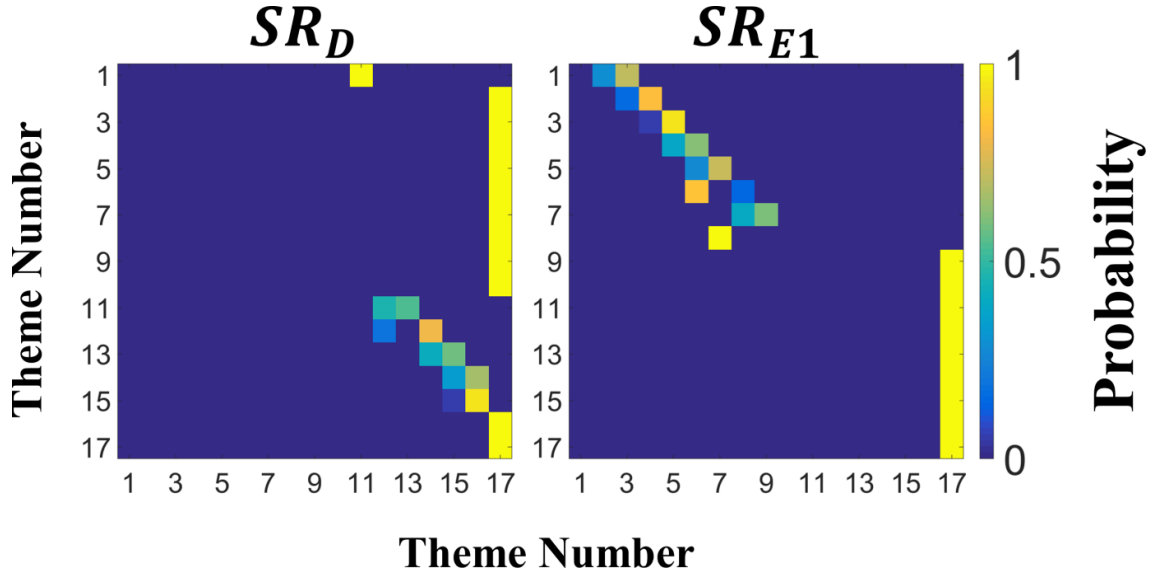


Figure 3.2. Representation of the two SR song types (SR_D, west Australia and SR_{E1}, east Australia) with their relative transition probabilities indicated in different colours. Each theme number is identified by the numbers on the x and y axis.

This approach allowed the presence of SRs that potentially can produce both song types. Excluding the start and end themes (1 & 17; Figure 3.2) the SR assigned to population E1 (SR_{E1}) most likely produced themes 2, 3, 4, 5, 6, 7, 8; 9 and 10; conversely, agents equipped with SR_D most likely performed themes 11, 12, 13, 14, 15 and 16. The non-zero theme transition probabilities for each row were manually located in close or adjacent cells to maintain an overall predictability of the song output, useful in order to track song types across the model's iterations. Once the overall structure of the matrix was manually designed (i.e. the location of each potential non-zero transition probability), for each decided matrix location the transition probabilities for both song types were determined by pulling a random number between 0 and 1; the sum of each SR matrix's row needed to be 1, therefore the pulled random number was subsequently subtracted from 1, in order to determine the transition probability of the adjacent cell. The only transition that did not follow this process was the 1 to 11 transition in SR_D which was equal to 1 from the beginning. This was done because this transition was used as a bridge between the two song types; making this transition probability equal to 1 precluded entirely the production of the themes of SR_{E1}. On the other hand, if the 1 to 11 transition probability was lower than one, then the agents could potentially produce both song types. However, due to the use of this bridge transition (1 to 11) between the

two song types, the agents could not produce hybrid songs that contained, within the same song sequence, themes belonging to both song types (Garland et al., 2017a). The repertoire of songs produced using SR_D was set to represent the revolutionary song type in this two-populations modelling system. To track diffusion of the revolutionary song type in the different modelling scenarios, theme 11 was used as a 'marker' to track the frequency of SR_D songs across both populations in each model iteration. Across modelling scenarios, I considered a song revolution to have occurred whenever the SR_D song type replaced completely SR_{E1} song type within two migration cycles (Noad et al., 2000).

3.3.4. Song Learning Rules

The basic assumption of chapter 2 regarding modelling transmission loss and hence learning salience as a function of distance was maintained. I still calculated song intensity (I) as $1/d^2$ where d was the Euclidean distance between singer and listener agents. The basic song learning mechanism remained the same: a listener agent received the song sequence of a singer agent, estimated the SR based on the theme sequence, and updated its SR as a function of the estimated SR, the received intensity *I*, and the learning rule in place.

3.3.4.1. Model 1: Distance-only

The distance-only learning rule (model 1) was explored and tested in depth in the experiments presented in the previous chapter. It was designed to be a baseline condition because it made no assumptions about learning bias in humpback whales. Using the distance only algorithm, song learning was a function of sound transmission loss, as seen in Equation 3.1:

$$SR_l' = SR_l * (1 - I) + (SR_s * I) \qquad \text{(Equation 3.1)}$$

where SR_l is the listener's original transition matrix, and SR_s is the transition matrix that the listener estimates from the realised song sequence produced by a singing agent, I is the received intensity, and SR_l' is the updated transition matrix of the listener. For the set of experiments presented here model 1 was used to both explore alternative

geographic scenarios compared to chapter 2 as well as a control when other types of learning biases were used.

3.3.4.2. Model 2: Distance + Novelty bias

Model 2 was developed to explore the potential role of novelty bias in the emergence of song revolutions. It worked on the assumption that more novel (or unexpected) songs might be positively selected by females, making them more desirable learning targets for males, and therefore causing them to spread quickly across a population (Todd and Werner, 1999; Noad et al., 2000; Garland et al., 2011). A novelty value, α, was computed as

$$\alpha = \frac{\sum_{n}^{N-1} SR_{Song_n,m} - SR_{Song_n,Song_{n+1}}}{N-1} \qquad \text{(Equation 3.2)}$$

where SR is the listener agent SR matrix, $Song$ is the song sequence α is being calculated, n is the current index of the song sequence ($Song$), N in the total length of the song sequence and m is the most probable transition in row $Song_n$. Effectively, α is a measure of the difference between the theme transition an agent expects to hear based on its own SR and the transition probability an agent actually hears, estimated from the singer's song sequence. Novelty (α) was then multiplied by received intensity (I) to create the weight in the SR weighted average algorithm (Equation 3.3)

$$SR_l' = SR_l * \left(1 - (I * \alpha)\right) + SR_s * (I * \alpha) \qquad \text{(Equation 3.3)}$$

3.3.4.3. Model 3: Distance + Song Memory

The first step in introducing a memory bias into the model architecture was to define the structure in which the agent's memory was going to be stored. I designed the memory song representation (MSR) as a transition matrix the same size as the agent's SR matrix (17x17). Each agent stored in its MSR an aggregated representation of the theme transitions produced by singer agents surrounding him. At each model iteration, a listener agent computed an estimated transition matrix from a song produced by each singer agent which was multiplied by the singer's intensity factor (I) and then averaged

with the listener's memory SR (MSR_l) using a matrix weighted average algorithm. Thus the updated memory SR of listener *l*, $MSR_l{}'$, after hearing singer *s*, was given by

$$MSR_l' = (c * MSR_l) + \big((1 - c) * (SR_s * I)\big), \qquad \text{(Equation 3.4)}$$

where MSR_l is the listener's previous memory SR, *c* is the memory conservatism parameter (described in more detail below), SR_s is the estimated song representation matrix for singer *s*, and *I* is the intensity factor associated with singer *s*. This calculation was carried out by each agent taking turns as the listener, as in chapter 2. The result was an updated memory ($MSR_l{}'$) that incorporated the theme transitions of the songs sung by the singer agents around the listener, mediated by their distance from the listener, representing a summary of the overall song-scape the agent had been exposed to in that iteration of the model (Figure 3.3).

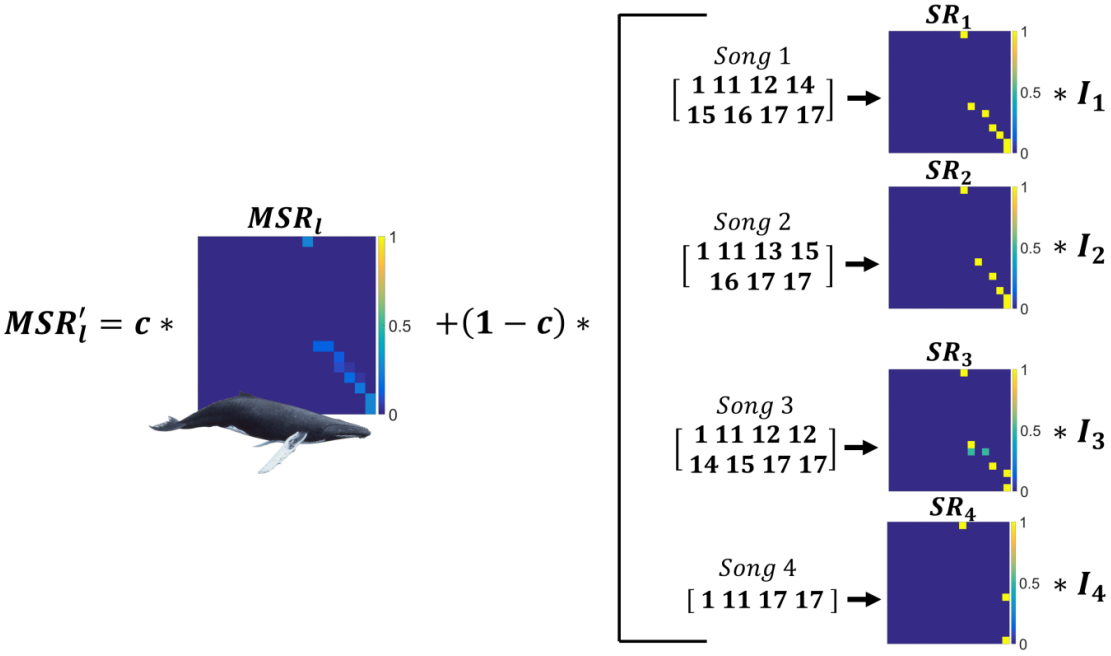


Figure 3.3. Graphic representation of the song memory construction process using Equation 3.4. Here *c* represents the memory conservativism constant, and MSR_l is the listener memory SR. The vertical square bracket is used to group four singer agents the listener will use to update its memory SR ($MSR_l{}'$). One singer at the time, the listener estimates the singer's SR ($SR_{1\text{-}4}$) from the singer's song (*Songs 1-4*), this is then multiplied by its intensity factor defined by the distance of each singer from the listener ($I_{1\text{-}4}$). In this way each singer's effect on the listener memory is mediated by the singer's distance.

Equation 3.4 was weighted by a constant, c, representing how conservative an agent was when incorporating new songs into its memory. This parameter assumed values between 1 and 0. A high c would cause an agent to favor its pre-existing memory (MSR_l; Equation 3.3, Figure 3.3) over songs heard in the current iteration when updating its memory ($MSR_l{}'$; Equation 3.4, Figure 3.3). Conversely, a low c would result in a higher relative impact of newly heard songs over the preexisting memory, skewing $MSR_l{}'$ towards more recent memory (i.e. the songs produced in the last iteration).

Once the memory structure was in place (*MSR*) and the algorithm to update it was working ($MSR_l{}'$; Equation 3.4), it was necessary to specify how the agent's memory influenced its learning. In order to do so, I calculated a value, termed 'conformity mismatch' (CM), that encapsulated the degree of match between the agent's current SR and its memory (MSR). CM was calculated through a three step procedure. (1) The two-dimensional correlation coefficient r between an agent's SR and MSR was calculated as:

$$r = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}(SR_{ij}-\overline{SR})(MSR_{ij}-\overline{MSR})}{\sqrt{\sum_{i=1}^{m}\sum_{j=1}^{n}(SR_{ij}-\overline{SR})^2 \sum_{i=1}^{m}\sum_{j=1}^{n}(MSR_{ij}-\overline{MSR})^2}}, \qquad \text{(Equation 3.5)}$$

where $\overline{SR}$ and $\overline{MSR}$ are the means of the elements of SR and MSR respectively (these latter having dimentsons m and n – in this case *m*=*n*=17). The resulting two-dimensional correlation coefficient r ranged from -1 to 1. (2) This was then transformed to a value between 0 and 1 to give $rNorm$, as follows:

$$rNorm = \frac{(r+1)}{2} \qquad \text{(Equation 3.6)}$$

Finally, (3) the conformity score for each agent was calculated by squaring $rNorm$ and subtracting it from 1 (Equation 3.7):

$$CM = 1 - (rNorm^2) \qquad \text{(Equation 3.7)}$$

The conformity mismatch (*CM*) was therefore an estimation of the degree of correlation between what an agent was currently singing (i.e. its SR) and what the agents around him had been singing during the preceding model iterations (i.e. its

MSR). To give an illustrative example consider an agent that has been in the same population for some time. They would would have a current SR that mirrored very precisely its MSR (first row; Figure 3.4). However, that agent came into contact with the songs of agents from another population then the correlation between its current SR and its MSR would be lower, resulting in a higher CM value (second row; Figure 3.4).

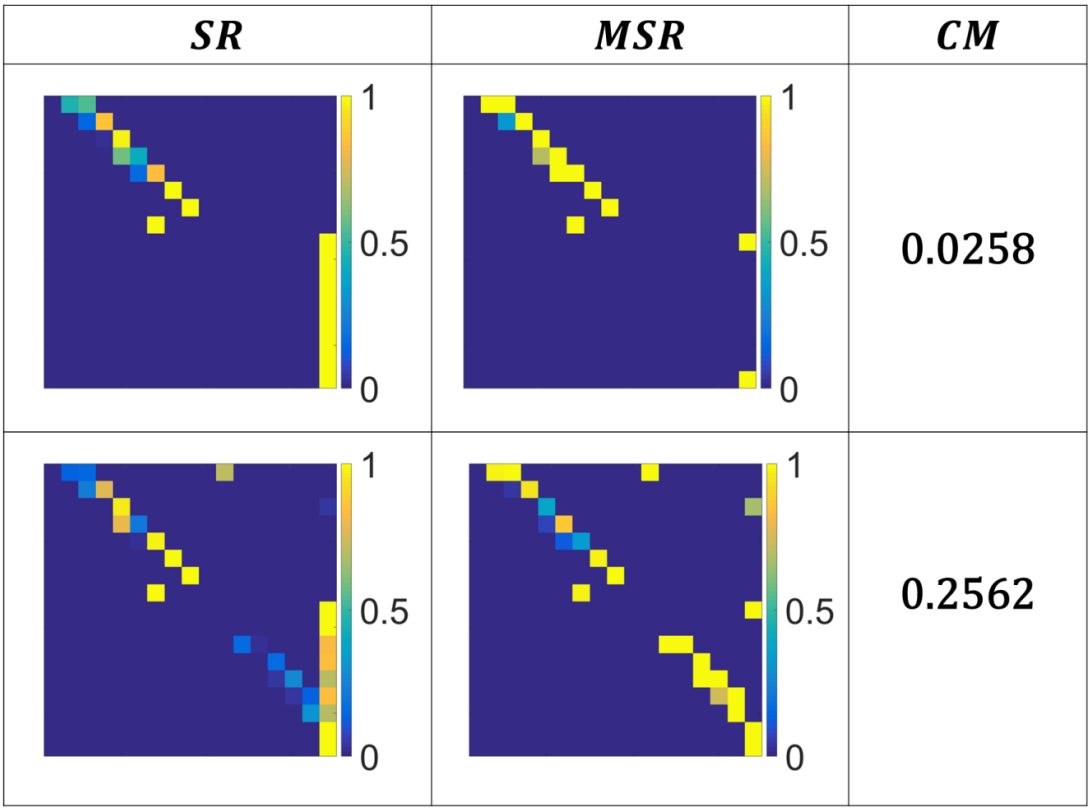


Figure 3.4. Two examples of conformity mismatch (*CM*) values with the respective SR matrices and memory SRs (MSR) used to calculated them. The first row represents an example in which the agent never left its population of origin, where its SR will therefore match its MSR resulting in a low *CM*. The second row represents the situation in which the agent has been exposed to a new song type. The theme transitions from the new song type are stored in the agent's MSR, increasing the mismatch between the current SR and MSR. (Note that due to the fact that MSRs are multiplied by the singers' intensity factors, their transition probabilities are usually low and here for visualisation purposes I used MSRs with unrealistically high transition probabilities).

In model 3, the agent's *CM* value then affected the agent's song learning algorithm , where $SR_l{}'$, the updated song representation of listener *l*, after hearing singer *s*, was given by:

$$SR_l' = SR_l * \left(1 - (I * CM_l)\right) + SR_s * (I * CM_l) \qquad \text{(Equation 3.8)}$$

where SR_l is the listener's SR matrix, and SR_s is the singer's SR as esimated by the listener. The learning weighting was formed by multpling the received intensity (I; i.e. singer's distance) with the listener conformity mismatch (CM_l). Both the singer's distance and the listener's conformity mismatch could then affect the listener's learning process and its updated SR (SR_l'). A low CM_l would limit the listener agent's learning, increasing the influence of its own SR (SR_l) on its updated SR (SR_l'). Conversely, a higher conformity mismatch (CM_l) would enhance the effect of singer's song (SR_s) on the listener updated SR (SR_l'), effectively pushing the listener to learn more from the singer. Thus an agent with a current song that matched those it had been hearing in the past would be disinclined to learn, while an agent whose song and memory were mistmatched would learn more readily.

3.3.5. Parameter Space and Model Analysis

The aim of this chapter was to test different modelling scenarios and learning biases to understand what set of parameters and learning rules could lead to the emergence of song revolutions. In all simulations, I used two populations of agents (termed D and E1) that possesed different initial SRs (SR_D and SR_{E1}). In the analysis presented here I tested three movement scenarios in combination with three distinct learning biases.

The parameter space for the experiments presented here remained mostly unchanged compared to chapter 2 (Table 3.1). The model experiments were run for two migration cycles (12000 iterations each); each experiment was run with a total of 30 agents subdivided into the two populations, D and E1. The precise division depended on which of the movement scenarios was being tested. In the first movement scenario the sizes of populations D and E1 were set to 20 and 10 agents respectively. This was done to represent the relative difference in population size between the western and eastern Australian populations (Noad et al., 2011; Salgado Kent et al., 2012), so as to explore whether a simple difference in population size could explain revolution events. In the second and third movement scenarios both population D and E1 comprised 15 agents each because I wanted the initial memory states of the two populations to be comparable

(that is, agents in each population should have experienced the same interactions between song, memory, and conformity mismatch). Since differences in agent density between the two populations' breeding and feeding areas could potentially lead to variable song exposure and therefore differences in MSR formation, the populations needed to be the same size. Across all scenarios, multiple breeding and feeding ground sizes were tested. The first movement scenario included 5 sets of experiments, for each of these sets I tested five different breeding (BGS) and feeding ground sizes (FGS), from size 10 to size 50. This parameter space was designed to test if the interplay between agents' density (BGS & FGS), population size and population differences could allow for the emergence of song revolutions using a distance-only learning bias. In movement scenarios 2 and 3, I tested two BGS & FGS sizes (5 and 50). Based on chapter 2's results, across all scenarios, the zone of repulsion (ZOR) and the zone of attraction (ZOA) were kept fixed at 0.1 and 1 respectively. The singing probabilities across different parts of the experiments were kept unchanged compared to chapter 2, with the exception of a set of models in which the feeding season singing probability (P_s) was increased to match that on the breeding ground. This set of experiments was used to test whether an increased singing activity led to a higher song revolution occurrence.

Table 3.1. Parameter setting use across all the three movement scenarios tested

Parameter name	Parameter value
Number of iterations (*i*)	24000 12000 for each migration cycle
Number of migration cycles	2
Population size	**30 agents total**
	Scenario 1: Population D: agents 1-20 Population E1: agents 20-30
	Scenario 2: Population D: agents 1-15 Population E1: agents 15-30
	Scenario 3: Population D: agents 1-15 Population E1: agents 15-30
Breeding Ground Size (BGS)	5, 10, 20, 30, 40, 50
Feeding Ground Size (FGS)	5, 10, 20, 30, 40, 50
Zone of Repulsion (ZOR)	0.1
Zone of Attraction (ZOA)	1
Maximum song length	50 themes
Song representation (SR) matrix size	17 by 17
Memory song representation (MSR) matrix size	17 by 17
Singing probability depending on iteration number (*i*) (P_s)	i0-i2000 = 0.5 (migration) i2000-i6000 = 0.8 (breeding grounds) i6000-i8000 = 0.5 (migration) i8000-i12000 = 0.08 and 0.8 (feeding grounds)
Memory conservatism (*c*)	0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 0.999

I ran 7500 model experiments in total, 2500 in the first movement scenario, 2500 in the second and 2500 in the third. Each set of parameters was run 100 times to avoid biased results due to the inherent stochasticity of this modelling approach. For each experiment, SR_D song frequency was calculated every 100 iterations and the median for each pool of 100 experiments was then estimated to understand the general trends. SR_D song frequency was indicated in the following figures on a scale from 0 to the total number of agents in each population, depending on the different movement scenarios (Table 3.1).

3.4. Results

3.4.1. Movement Scenario 1

In this scenario SR_D song frequency had an initial baseline of 20 (i.e. the size of population D; for visualisation, the y-axis scale is focused on population E1 (i.e. the interval 0 to 10; Figure 3.5). An SR_D song frequency of 0 suggested that the revolutionary song type did not diffuse across population E1 while a frequency of 10 indicates that all the agents in population E1 had songs originating from SR_D (i.e. a song revolution occurred).

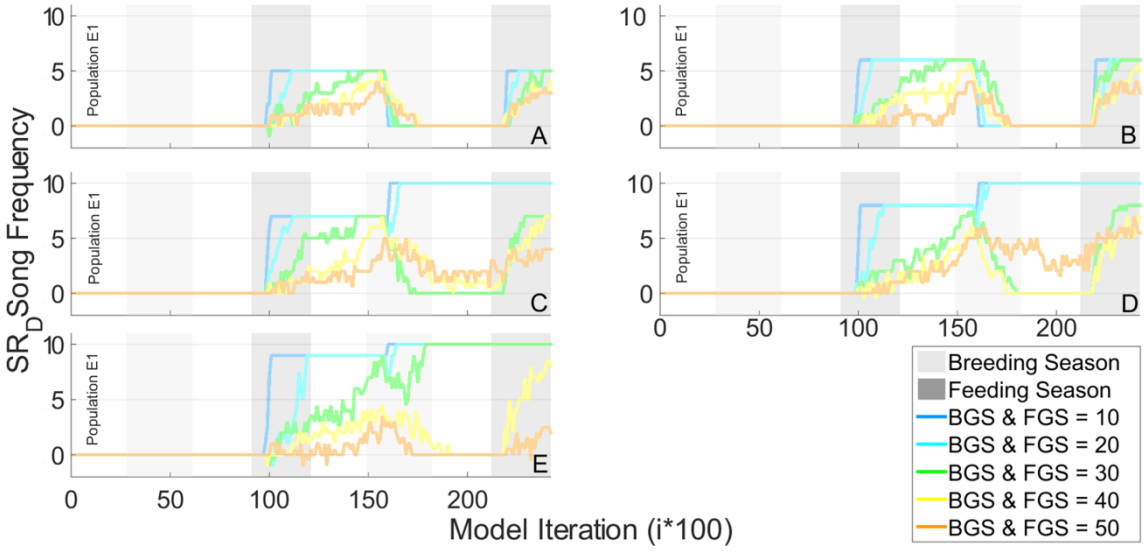


Figure 3.5. The extent of feeding ground overlap affects the probability of song revolutions when no learning biases are present. Median SR_D song frequencies across the five distinctive set of model 1 experiments (A – E) with five BGS & FGS each (10, 20, 30, 40, 50) represented with different colours. The five sets represented different proportions of population E1 spatially overlapping with population D in area IV. A: 50%; B: 60%; C: 70%; D: 80% and E: 90%.

Across all experiments in this scenario the speed of diffusion of the revolutionary song SR_D in population E1 was mostly influenced by the size of breeding and feeding areas. Small BGS & FGS (10 & 20; Figure 3.5) lead to abrupt increases in SR_D song frequency while for larger BGS & FGS, song diffusion occurred more gradually over a larger number of iterations. During the first feeding season, agents of population E1 migrating to area IV acquired SR_D song from the agents of population D; subsequently, during the second breeding season they transmitted the novel songs to the remaining agents of population E1 that spent the previous feeding season isolated in area V; when song revolutions occurred they always did during the second breeding season of the two migration cycles. In the two experimental sets in which 50% and 60% of population E1 mixed with population D (Figure 3.5 A & B) some E1 agents learnt the revolutionary song but no revolutions occurred. When the proportion of population E1 interacting with D was increased to 70% and 80% however, song revolutions started to occur consistently with breeding and feeding grounds of size 10 and 20 (Figure 3.5 C & D). Finally, if 90% of population E1 interacted during the feeding season with

population D, song revolutions occurred consistently even with larger breeding and feeding grounds (BGS & FGS = 30 and partially 40; Figure 3.5 E).

3.4.2. Movement Scenario 2

The second movement scenario was initially tested using model 1 (distance-only), model 2 (distance + novelty) and model 3 (distance + memory). In the following figures, SR_D song frequency is plotted between 0 and 15 for each of the two populations (15 = maximum number of agents for each population). The three learning biases were compared using the same set of parameters. With BGS & FGS = 5, model 1 (distance-only) produced some abrupt increases in SR_D song frequency, from 0 to 15, but in the majority of cases, the immigrant agent of population D conformed quickly to the new SR_{E1} song majority of population E1 (the median SR_D song frequency in population D decreased in this case from 15 to 14; Figure 3.6). Upon returning to its original breeding areas (population D) the agent reacquired the new majority SR_D song, hence the increase in median frequency from 14 to 15 (thick black line; Figure 3.6). SR_D song frequency when model 2 (distance + novelty) was used followed a different pattern. During the first feeding season, the frequency of the revolutionary song in population E1 increased and stabilised at around five agents (SR_D song frequency = 5, i.e. ≈ 30% of E1 population; Figure 3.6). However, during the second breeding season SR_D song frequency decreased within population D resulting in SR_{E1} songs diffusing to ≈ 30% of agents of population D (SR_D song frequency = 10; Figure 3.6), representing a partially inverse or failed revolution going in the opposite direction than the temporary immigration.

The implementation of model 3 (memory conservatism c = 0.9, blue lines; Figure 3.6) led to a higher likelihood of song revolutions compared to the other two learning biases. During the first feeding season, the introduction of the immigrant agent from population D into population E1 feeding area triggered a steep increase in frequency of SR_D songs up to more than 60% of population E1 (SR_D song frequency = 10; Figure 3.6). After the agent from population D abandoned population E1 to return to its own population, the frequency of the revolutionary song stabilised at around 12 E1

agents during the northward migration and finally reached 100 % of the E1 during the breeding season of the second migration cycle (SR_D song frequency = 15; Figure 3.6).

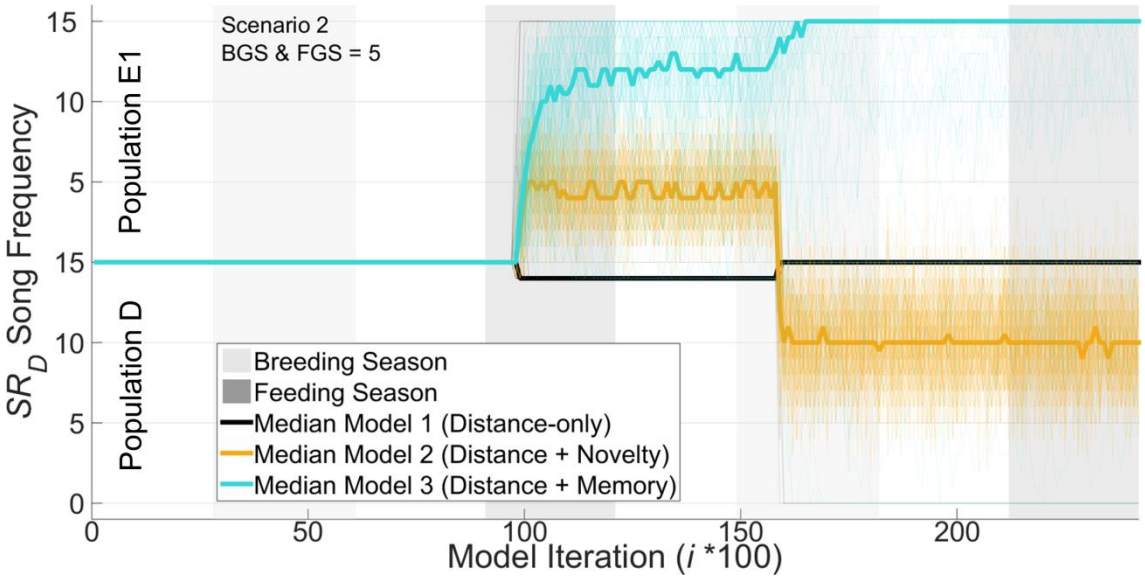


Figure 3.6. Song frequencies after temporary immigration. SR_D song frequency when the size of the breeding and feeding ground was set to 5 compared across three learning biases: distance-only (model 1; black lines), distance + novelty (model 2, yellow lines) and distance + memory (model 3, c = 0.9, blue lines). In movement scenario 2, one immigrant agent from population D mixed temporarily with population E1 during the first feeding season. Thick lines represent the median for each learning bias set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively.

With a larger BGS & FGS (50) the overall frequency pattern of the revolutionary song using model 1 did not change compared to the smaller ground size (Figure 3.7). However, the SR_D song frequency variability between experiments increased, with some runs resulting in song revolutions in population E1 (SR_D song frequency = 15) and others in complete inverse revolutions where the SR_{E1} songs diffused into population D (Figure 3.7). Model 2 results were broadly similar to those under a small BGS & FGS. The initial increase in revolutionary song frequency was slower with a larger BGS & FGS, but during the second breeding season SR_D songs frequency decreased in population D similarly to results using smaller breeding and feeding grounds. The most notable change with larger BGS & FGS was in the outcomes of model 3 (thick blue line, c = 0.9; Figure 3.7). The decrease in agent density, driven by the increase in breeding and feeding ground size, impacted negatively on the

diffusion of the revolutionary song in population E1. Across multiple experiments, only about 30% of population E1 ever produced SR_D songs ($5 \leq SR_D$ song frequency ≤ 10; Figure 3.7), and the overall median frequency indicated an absence of song revolutions (SR_D song frequency in E1= 0; Figure 3.7).

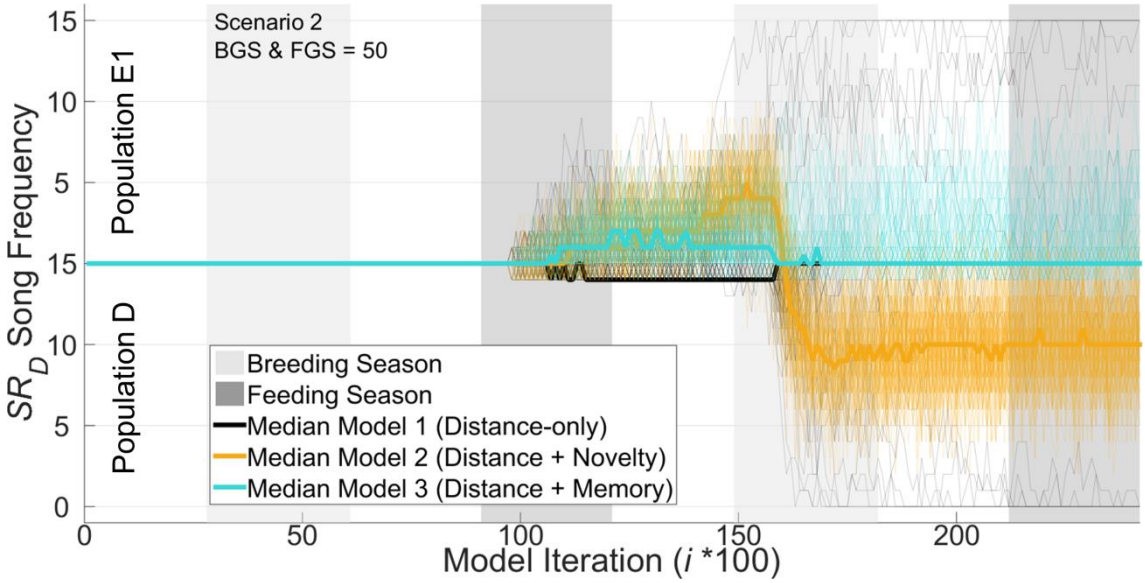


Figure 3.7. The effect of large feeding and breeding grounds on song frequency after temporary immigration. SR_D song frequency when the size of the breeding and feeding ground was set to 50 compared across three learning biases: distance-only (model 1; black lines), distance + novelty (model 2, yellow lines) and distance + memory (model 3, c = 0.9, blue lines). Thick lines represent the median for each learning bias set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively.

Once the differences between models 1, 2 and 3 were explored, the focus of the analysis shifted towards a more thorough testing of model 3 (distance + memory) and, more specifically, the effect of different values of memory conservatism (c) on the emergence of song revolutions in population E1. Ten different c values were tested, from low (0.1) to high (0.999) memory conservatism, for each c value, 200 experiments were run (100 with BGS & FGS = 5; 100 with BGS & FGS = 50) totalling in 2000 further model runs. Due to the large amount of resulting data, I present only the median SR_D song frequency for each c value (Figure 3.8); however, the results of all the individual model runs for all c values can be found in Appendix 3 (Figures A3.1 & A3.2).

The value of c, the memory conservatism parameter, strongly affected revolutionary song diffusion across population E1. A low c (0.1) produced a slight increase of SR_D song frequency in the beginning of the first feeding season, triggered by the arrival of the agent from population D into E1 feeding area V. However, this slight increase is then rapidly followed by a steady decrease resulting in the immigrant agent conforming to the SR_{E1} song repertoire (SR_D song frequency in population D = 14; Figure 3.8). Higher c values (0.2, 0.3, 0.4 and 0.5) generated higher revolutionary song frequency peaks that nonetheless ultimately resulted in the disappearance of the revolutionary song type in population E1 once the agents reached their breeding areas (SR_D song frequencies in population E1 = 0; Figure 3.8). In experiments where c = 0.6 the revolutionary song median frequency reached roughly 60% of population E1 (SR_D song frequency ≈ 10; Figure 3.8) at the end of the first feeding season to subsequently decrease towards ≈ 50% of the E1 population; in this case population E1 produced consistently both SR_D and SR_{E1} songs. Runs with c values higher than 0.7 predominantly produced song revolutions in population E1 (SR_D song frequency = 15; Figure 3.8). Revolutionary song frequencies for this set of c values showed sharp increases during the first feeding season followed by the completion of the song revolution events during the second breeding season of population E1. At this stage the immigrant agent from population D already returned to its original population, indicating that, given enough memory inertia, revolutions could occur even if the interaction between the immigrant agent and population E1 is limited to a single feeding season.

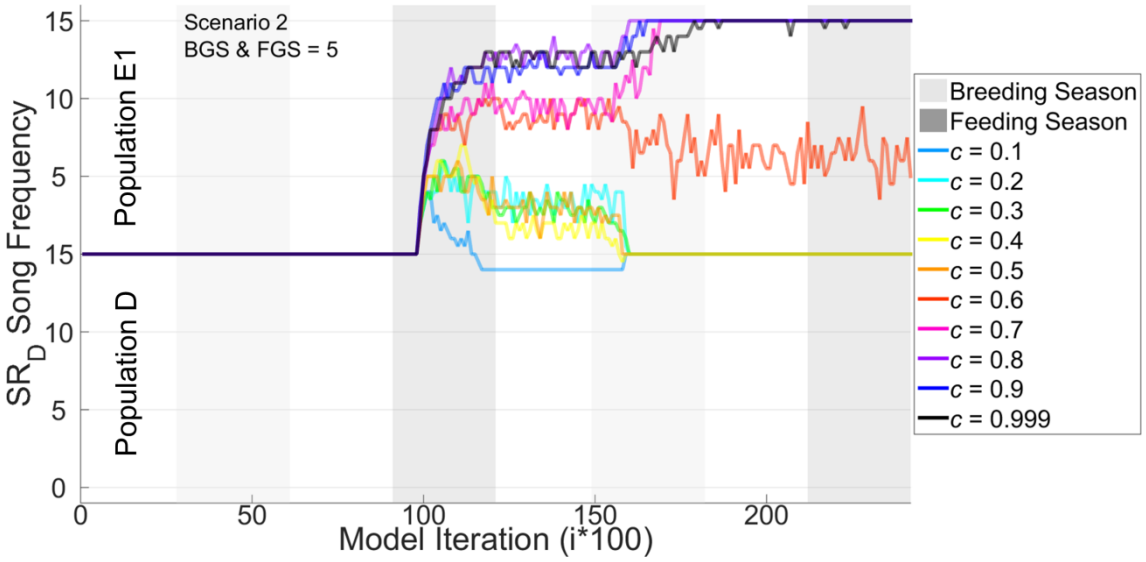


Figure 3.8. Memory conservatism affects song frequencies after temporary immigration. Median SR_D song frequencies compared across ten distinct c values (from 0.1 to 0.999) each indicated with a line of different colour. The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding grounds was set to 5.

Model 3 experiments run with larger breeding and feeding grounds (BGS & FGS = 50) did not display song revolutions at any c value (Figure 3.9). The arrival of the immigrant agent in population E1 feeding area triggered a slight increase of SR_D song frequency ($0 \leq SR_D$ song frequency in E1 ≤ 2; Figure 3.9); however, once population E1 started its northward migration SR_D songs disappeared almost entirely from its song repertoire.

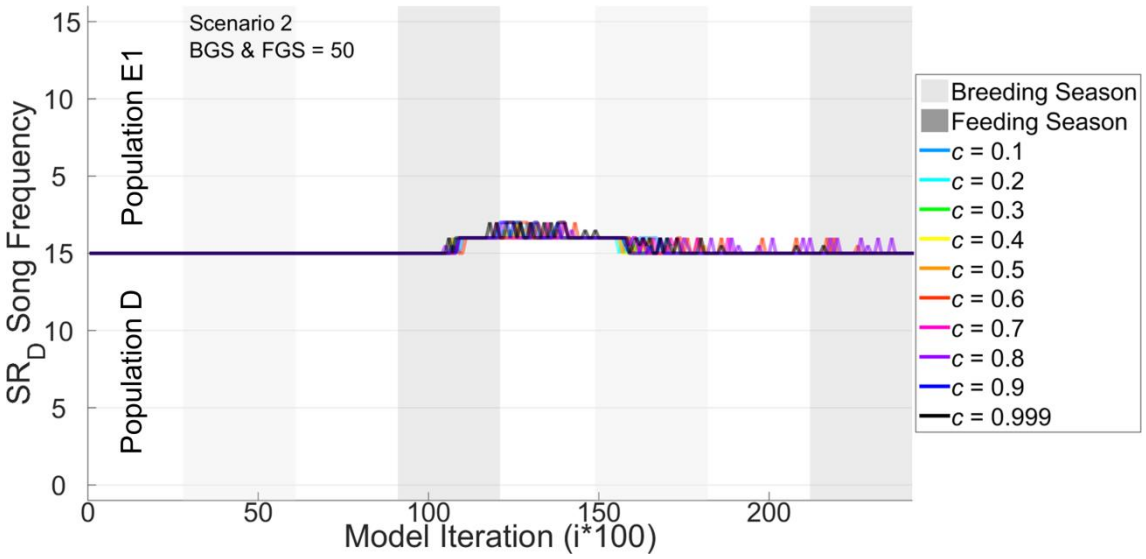


Figure 3.9. Increased memory conservatism does not rescue revolutions when feeding and breeding grounds are large. Median SR_D song frequencies compared across ten distinct c values (from 0.1 to 0.999) each indicated with a line of different colour. The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding grounds was set to 50.

3.4.3. Movement Scenario 3

In the movement scenario 3 the immigrant agent from population D that spent the feeding season in the feeding area V (E1 feeding area, Figure 3.1) joined the northward migration towards population E1's breeding ground, and remained with population E1 for the entire second migration cycle. Similarly to the analysis for the second movement scenario, models 1, 2 and 3 were initially compared using the same set of parameters, using both small (5) and large (50) breeding and feeding areas.

The revolutionary song frequency pattern using model 1 (distance-only) did not show great differences compared with movement scenario 2. Similarly to the previous scenario, in a few runs song revolutions in population E1 did emerge as soon as the immigrant agent from population D reached area V during the first feeding season (Figure 3.10). However, in the majority of cases the SR_D songs introduced by the immigrant agent did not diffuse in the E1 population. After the first feeding season, the immigrant agent generally permanently acquired the SR_{E1} song repertoire, abandoning its old songs (Figure 3.10). SR_D song frequency using model 2 (distance + novelty)

presented a stable pattern, without the decrease observed in scenario 2 (thick yellow line; Figure 3.10). This was because the immigrant agent did not return to its population of origin (population D). The implementation of the novelty bias did not produce any song revolutions in population E1 across all the 100 experiments run (Figure 3.10). The median SR_D song frequency using model 3 (distance + memory) presented a very similar trend to the one in scenario 2: a sharp increase in the frequency during the first feeding season followed by the finalisation of the song revolution during the second breeding season of the two migration cycles (thick blue line, SR_D song frequency = 15; Figure 3.10).

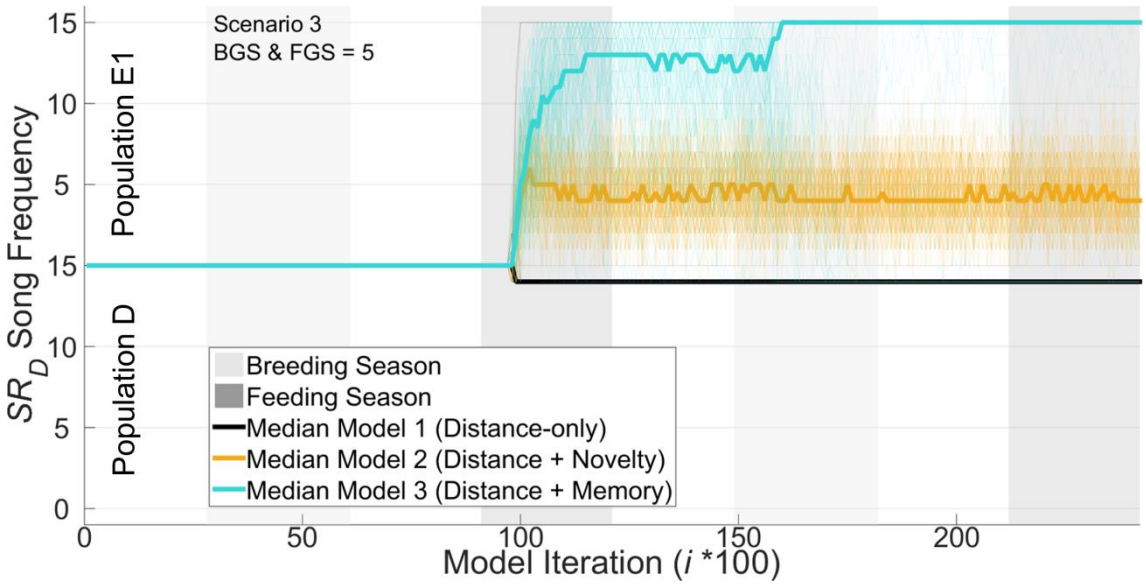


Figure 3.10. Song frequencies after long-term immigration. SR_D song frequency compared across three learning biases: distance-only (model 1; black lines), distance + novelty (model 2, yellow lines) and distance + memory (model 3, c = 0.9, blue lines). In movement scenario 3, one immigrant agent from population D joined permanently population E1 from the first feeding season till the end of the experiment. Thick lines represent the median for each learning bias set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding grounds was set to 5.

When model 1 was tested using larger breeding and feeding areas the frequency of the revolutionary SR_D in population E1 did not differ compared to BGS & FGS = 5 (Figure 3.11). Model 2 displayed a slower increase in song frequency due to lower agent spatial density but the pattern of SR_D song frequency values was extremely similar to results from smaller breeding and feeding areas (Figure 3.11). The greatest

difference between small and large breeding/feeding grounds was again seen in model 3's results. Similarly to the temporary immigration scenario, the decrease in agents' density prevented the emergence of song revolutions in population E1 (Figure 3.11). However, if compared to the same BGS & FGS experiments of the movement scenario 2 (Figure 3.9), the prolonged population switch of the immigrant agent had a notable effect on the frequency of the revolutionary song type in population E1. While in scenario 2 the median SR_D song frequency fluctuated around 0 (i.e. no agent of population E1 acquired SR_D), in scenario 3 SR_D songs diffused to ≈ 30 % of population E1 (SR_D song frequency ≈ 3; Figure 3.11).

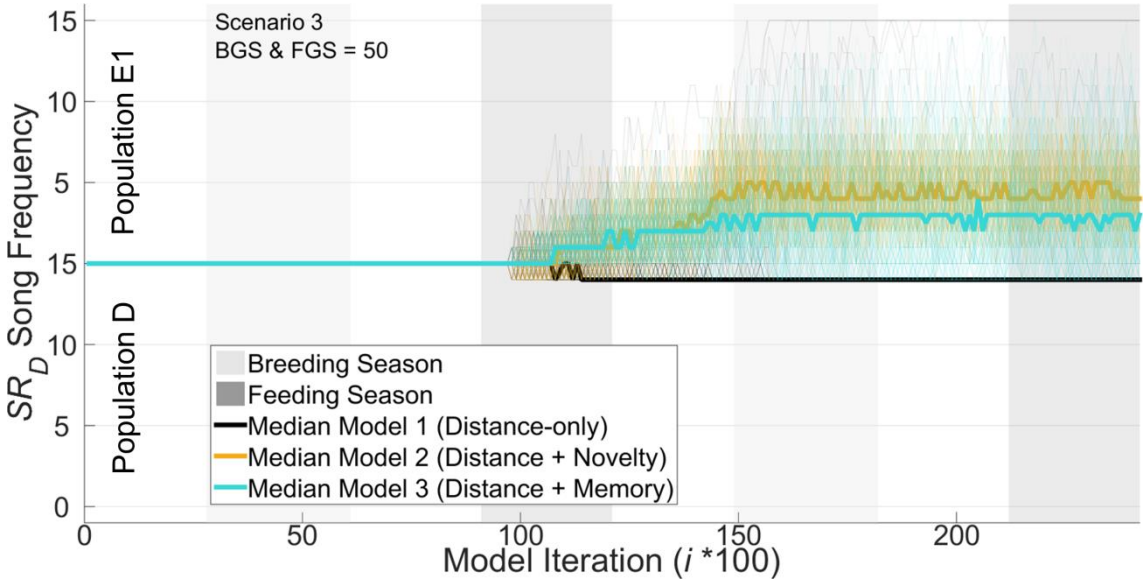


Figure 3.11. The effect of large feeding and breeding grounds on song frequency after long-term immigration. SR_D song frequency compared across three learning biases: distance-only (model 1; black lines), distance + novelty (model 2, yellow lines) and distance + memory (model 3, c = 0.9, blue lines). Thick lines represent the median for each learning bias set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding grounds was set to 50.

The patterns of median SR_D song frequency across the different memory conservatism (c) values can be grouped in three qualitative categories. First, runs where $c \leq 0.3$ displayed revolutionary song frequencies that rapidly decreased in population E1 after introduction by the immigrant agent during the first feeding season (Figure 3.12). Second, memory conservatism values that ranged between 0.4 and 0.6 resulted in a greater increase in frequency during the first feeding season, and a stabilisation around

30% of population E1 (SR_D song frequency ≈ 5; Figure 3.12), followed by a decrease of the frequencies once the agents reached E1 breeding ground during the second migration cycle. Thirdly, similarly to results under movement scenario 2, experiments with $c \geq 0.7$ generally produced SR_D song revolutions; the revolutionary song frequency reached 100 % of population E1's agents during the breeding season of the second migration cycle (Figure 3.12).

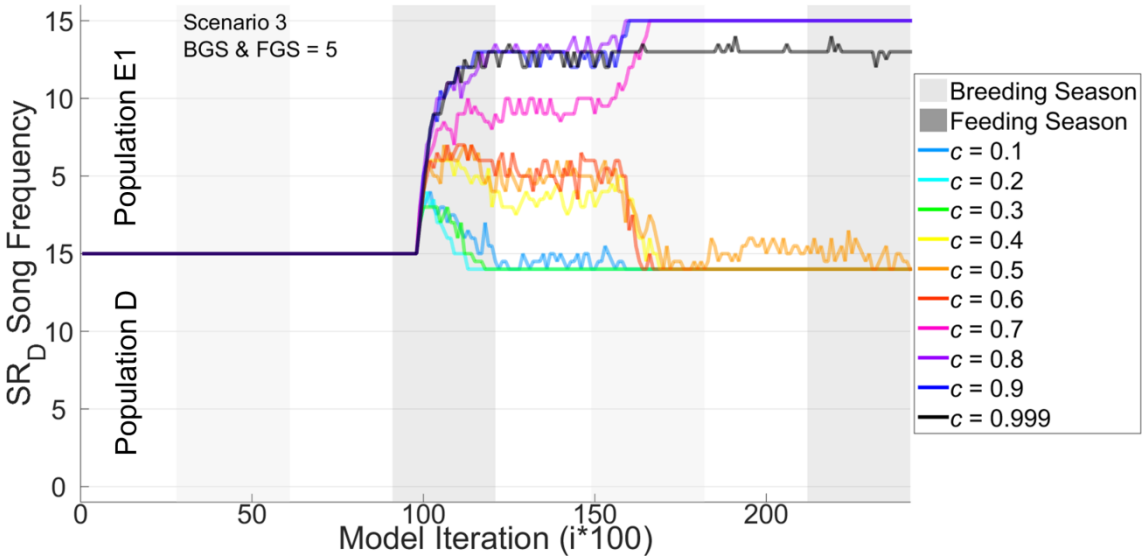


Figure 3.12. Memory conservatism affects song frequencies after long-term immigration. Median SR_D song frequencies compared across ten distinct c values (from 0.1 to 0.999) each indicated with a line of different colour. The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding grounds was set to 5.

Similar to results from the short term immigration scenario, when agent density decreased due to larger ground sizes (BGS & FGS = 50) the distance + memory learning bias was not as effective in triggering song revolutions. Median SR_D song frequencies never exceeded 30% of the E1 population regardless of c level ($0 \geq SR_D$ song frequencies ≥ 5; Figure 3.13). The permanent switch of the immigrant agent during the whole second migration cycle had only a minor effect on revolutionary song frequencies at all c levels compared to the previous movement scenario (Figure 3.13).

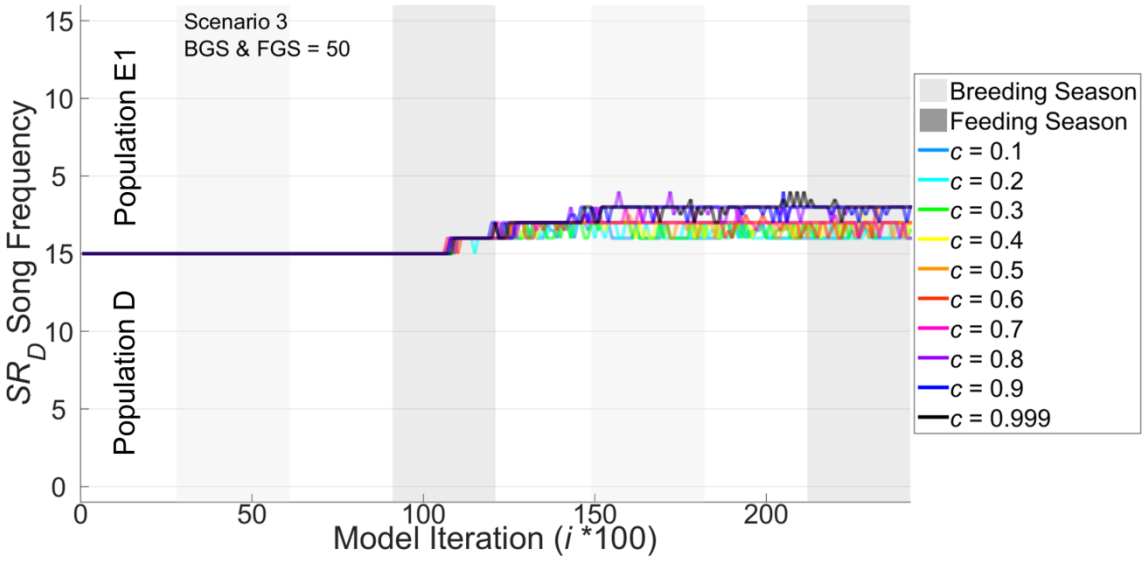


Figure 3.13. Increased memory conservatism does not rescue revolutions when feeding and breeding grounds are large, even when immigration is permanent. Median SR_D song frequencies compared across ten distinct c values (from 0.1 to 0.999) each indicated with a line of different colour. The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding grounds was set to 50.

3.4.4. High vs Low Feeding Season Singing Probability

The difference in the amount of singing occurring in humpback whale feeding and breeding grounds is still debated (Mattila et al., 1987; Stimpert et al., 2012; Vu et al., 2012; Garland et al., 2013a; Stanistreet et al., 2013; Magnusdottir et al., 2015; Español-Jiménez and van der Schaar, 2018). Therefore I carried out a further test with model 3 to estimate the effect of singing probability during the feeding season on the emergence of song revolutions. The memory conservatism and the size of feeding and breeding grounds were set to 0.9 and 5 respectively, for all the 400 experiments run. Both movement scenarios 2 and 3 were tested with a feeding season singing probability of 0.08 (i.e. the original runs) and compared to results where the feeding season singing probability was equal to the breeding season, at 0.8 (Figure 3.14).

Compared to results from a low singing probability of 0.08 during the feeding season, a high singing probability (0.8) made revolutions much less likely to occur. In both scenarios there was an initial increase in SR_D song frequency during the first feeding season; in few cases this resulted in SR_D song frequency spreading quickly to

all the agents of population E1 but in the majority of cases this was not enough to drive song revolutions. Before the end of the first feeding season the immigrant agent from population D conformed to SR_{E1} song repertoire; subsequently, it either moved back to population D resulting, in a few cases, in inverse revolutions, in which SR_{E1} songs diffused in population D (Scenario 2; Figure 3.14), or it just conformed to SR_{E1} (Scenario 3; Figure 3.14). Hence increased singing probability on the feeding grounds reduced the occurrence of song revolutions dramatically.

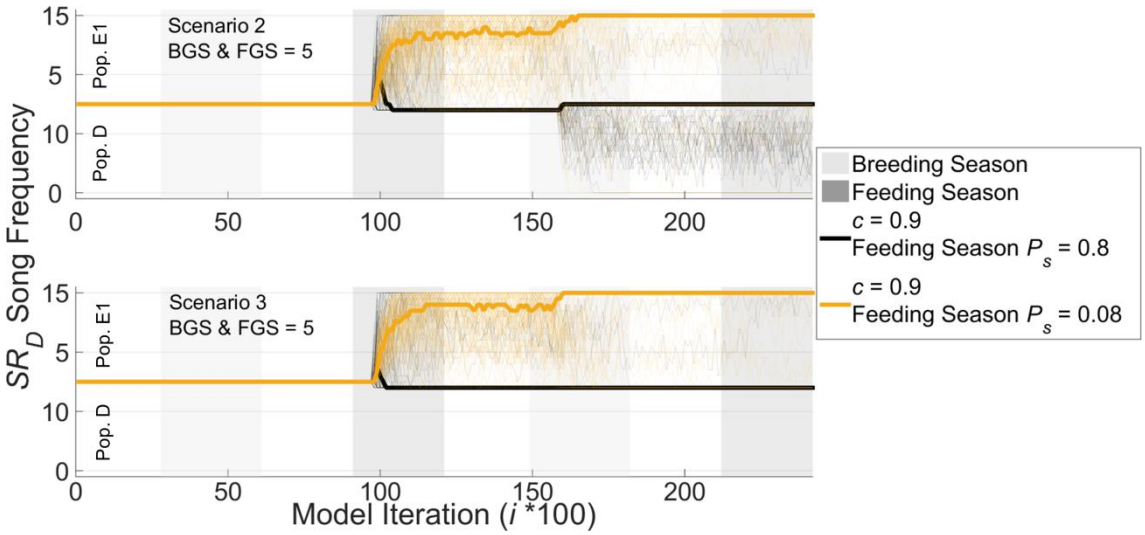


Figure 3.14. High singing rates on feeding grounds suppresses song revolutions. SR_D song frequency compared across two parameter setting for each of the two movement scenarios (2 and 3). Black lines represented experiments in which the singing probability during the feeding season was the same as the one during the breeding season (0.8). Yellow lines represented experiments in which the singing probability during the feeding season was one order of magnitude lower than the one during the breeding season (0.08). For both sets c value was set at 0.9. Thick lines represent the median for each set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding ground was set to 5.

3.5. Discussion

In this chapter I investigated how individual level movements, learning dynamics and biases could lead to humpback whale song revolutions, using spatially explicit agent-based models. I built upon the modelling framework and results of the previous chapter by introducing new geographical and movement scenarios, and giving agents both a memory of heard songs and a sense of how well or not their own songs

fitted with their current population context. I found that song revolutions could occur when learning was mediated by sound transmission loss only when significant portions (that is, at least 70%) of the two simulated populations spatially overlapped during the feeding season. If the spatial interaction between the two populations was constrained to the movement of individual agents, then song revolutions occurred only when agents were equipped with a song memory. In model experiments in which (1) agents were highly conservative towards pre-existing memories, (2) agents' density in the feeding grounds was high, and (3) the feeding season singing probability was kept low, song revolutions emerged consistently.

3.5.1. Movement Scenario 1

The first movement scenario was designed to explore the potential emergence of song revolutions whilst making the fewest assumptions possible regarding any learning biases or cognitive capacities in humpback whales. For this reason, all model experiments were run using learning mediated solely by distance (i.e. sound transmission loss; model 1). The results showed that song revolutions can occur without any specific learning bias, depending on the interplay between agents' spatial density in the breeding/feeding grounds, the ratio between the size of population D and E1 and proportion of migratory movements towards area IV by population E1's agents. This only occurred however when at least 70% of the E1 population migrated to a shared feeding ground.

There were two major assumptions built into scenario 1. The first was that the population sizes estimated in the breeding grounds of West and east Australia (Hedley et al., 2011; Noad et al., 2011) corresponded to the population sizes in the respective feeding grounds (i.e. the populations did not disperse to multiple feeding grounds). Recent population estimates for area IV (2001/2002) and V (2004/2005) seemed to align to the breeding ground estimates showing breeding stock D more than twice the size of breeding stock E1 (Matsuoka et al., 2011). The second assumption, that large portions of the E1 population overlapped with breeding stock D in area IV, was less realistic. Robust evidence across multiple studies (discovery tags, photo-id) shows that the two populations predominantly migrate to different feeding areas (Chittleborough,

1965; Franklin et al., 2012; Constantine et al., 2014). Thus having 70% of one population in another's principal feeding ground seems a highly unlikely occurrence.

However, there are also some considerations that have to be taken into account when interpreting movement scenario 1's results. The distribution of baleen whales across the Antarctic tend to be tightly correlated with the Southern Boundary of the Antarctic Circumpolar Current (ACC) (Tynan, 1998). In area IV and V, the late summer distribution of humpback whales was correlated with offshore areas of high productivity coinciding with the Southern Boundary (Tynan, 1998; Murase et al., 2002; Weinstein et al., 2017); these highly suitable areas for humpback whales to feed can vary both within and between feeding seasons (Bombosch et al., 2014), potentially increasing the chances for two adjacent populations to interact. Across the Western South Pacific, a consistent pattern of song transmission has emerged when a large population has overlapped on feeding and/or migratory areas with a smaller population: the song type produced by the larger population is usually transmitted to the smaller population within one feeding season. A good example of this yearly song transmission pattern was represented by the interaction between the large eastern Australian population (N = 14,522, CI= 12,777 – 16,504; Noad et al., 2011) and the small and adjacent New Caledonian population (N = 533, CV = 0.15; Garrigue et al., 2004). Song types recorded in the eastern Australian population were consistently recorded one year later, in New Caledonia (Garland et al., 2011; Garrigue et al., 2015). The fact that this type of yearly song transmission does not happen between the western and eastern Australian populations would indicate that the spatial overlap between these two populations is inconsistent, but potentially driven by slower processes with multi-year cycles.

Large scale climatic processes such as ENSO (El Niño-Southern Oscillation) or/and Southern Annular Mode (Murphy et al., 2007) as well as intraspecific competition (Ryabov et al., 2017) have a profound effect on Antarctic krill biomass cycles; these cyclic increases and decreases in krill biomass occur with a frequency of 5 to 6 years, with variations larger than one order of magnitude (Ryabov et al., 2017). Furthermore, a recent study reported an inter-annual synchronous oscillation of two measures of Area V humpback whales adiposity with environmental variables and climate indices (Nash et al., 2018). The two adiposity markers indicated that in the

summer of 2010/2011, which was preceded by positive modes of SAM and ENSO, whales encountered poor feeding conditions; based on dietary signals the authors suggested that whales, in response to lower prey availability, might have diversified either their feeding ground locations or their prey choice, or both (Nash et al., 2018). Lower prey availability might increase the frequency of the long-range movements that humpback whales have been shown to perform between foraging patches in Antarctica (Friedlaender et al., 2006; Dalla Rosa et al., 2008), resulting in poorer physical conditions (Nash et al., 2018) and a higher probability of overlap with neighbouring populations. If the results of movement scenario 1 could be interpreted in terms of foraging patches, rather than the entire feeding ground, then the increased movement between low quality foraging patches where the song-scape was dominated by the larger breeding stock D could be at the origin of song revolutions in eastern Australia. Furthermore, an additional demographic aspect should be taken into consideration. Since 2000, both breeding stocks D and E1 increased at an annual rate of ≈ 10-12% (Hedley et al., 2011; Noad et al., 2011; Salgado Kent et al., 2012). As population sizes continue to increase the probability of feeding ground spatial overlap might increase as well. If this were to happen I predict that song revolutions in the eastern Australian populations will become more frequent, eventually reaching a yearly song transmission pattern similar to the one currently observed between the eastern Australian and the New Caledonian population (Garland et al., 2011).

3.5.2. Movement Scenario 2 & 3

Both these scenarios were tested using the distance-only (model 1) and distance + novelty (model 2) learning biases. While some model 1 runs showed the emergence of occasional song revolutions, no revolutions at all occurred using model 2, irrespective of the agent densities (BGS & FGS = 5 & 50). For both model 1 and 2 however, the median SR_D song frequency showed no signs of song revolutions. Furthermore, to confirm that song production errors did not have any influence on the occurrence of song revolutions I tested the current movement scenarios on models 3 and 4 of chapter 2 (distance + production errors and distance + novelty + production errors), without observing the emergence of any song revolutions (Appendix 3, Figure A3.3). These results demonstrated that the movement of just one lone individual into an adjacent

feeding ground (or feeding patch) was unlikely to trigger any song revolution with sound transmission loss or novelty bias as the only factors influencing learning.

The implementation of model 3 with the memory learning algorithm produced more variable results, ranging from no diffusion to complete revolutionary replacement of the E1 population's song. These results were influenced by three main parameters: agent density in breeding and feeding grounds (i.e. BGS & FGS), memory conservatism (c), and probability of an agent singing during the feeding season (P_s). When high agent density (BGS & FGS = 5) was combined with high memory conservatism ($c \geq 0.7$) and low feeding ground singing probability (P_s = 0.08), song revolutions emerged in the majority of model experiments for both movement scenarios 2 and 3. Conversely, lower agent density (BGS & FGS = 50) resulted in no revolutions, irrespective of the c value. Mechanistically, the combination of these three parameters allowed the emergence of song revolutions because it created an asymmetry in the agents' song memory acquisition. High agent density and the one-to-many spatial dynamic (i.e. one immigrant-many residents) present in the feeding grounds introduced a difference in the probability of song memory acquisition between the immigrant and the residents. In other words, at a high agent density and low singing probability, there was a higher probability for a resident to be close enough when the immigrant sang (and hence to store the immigrant song in memory) than the probability for the immigrant to find itself close enough to a singing resident and perform the same procedure.

This asymmetry in the acquisition of song memory between E1 residents and the immigrant agent was clearly visible when looking at an example of SR matrices and memory SRs (MSR) at different stages of the model experiments (Appendix 3, Figure A3.4). Furthermore, differential levels of song memory acquisition had distinct effects on the agents' conformity mismatch values (CM; Equations 3.4-3.7). Individual conformity mismatch (CM) was usually low at the end of the first breeding season for all agents (Appendix 3, Figure A3.5) due to the fact that during the breeding season both populations (and their respective song types) remained geographically isolated. However, once the immigrant agent mixed with population E1 introducing SR_D songs in the SR_{E1} song-scape of feeding area V, the individual conformity mismatch values (CM) of E1 residents increased abruptly; conversely, the CMs of the immigrant agent

increased more slowly due to the one-to-many spatial dynamic effect I explained above (Appendix 3, Figure A3.5). Increased CM enhances an agent's willingness to learn (Equation 3.8), and once the E1 residents were more driven to learn due to their high conformity mismatch values, the SR_D song produced by the immigrant agent had a higher probability of spreading, given a high degree of memory conservatism that helped the immigrant to maintain the learning asymmetry against the resident agents of population E1. Although the one-to-many spatial dynamic had a major role in the current set up, the feeding ground agent density was also a key parameter for the occurrence of song revolutions. This outcome is consistent with the results of the previous chapter, as well as with studies showing that high population density increased song sharing in songbirds (Lachlan and Slater, 2003; Fayet et al., 2014).

The second key parameter that had a major effect on the emergence of song revolution was the memory conservatism constant (c). Model runs where the agents were highly conservative towards their pre-existing song memory ($c \geq 0.7$) showed more consistent emergence of song revolutions. Conversely, when agents were less conservative ($c \leq 0.6$) and hence had memories more strongly influenced by recent experience, song revolutions were less frequent (Figures 3.8, 3.12 and A3.5 in Appendix 3). When song revolution occurred, the trajectory of the SR_D song frequency showed similarities to experimental studies in which an introduced behavioural trait diffused through a population of birds to establish a novel tradition (Aplin et al., 2015b). From the point of view of the diffusion mechanism, higher c values allowed the immigrant agent to be less influenced by the feeding ground song-scape (i.e. SR_{E1} songs) surrounding him upon arrival in feeding area V. The combination of high memory conservatism and differential probability of memory acquisition between immigrant and residents broke the learning symmetry discussed in the introduction, and increased the probability for the immigrant agent to transmit its SR_D song to the agents of population E1. Once the revolutionary song has been stored in E1 agents' memory, increasing their willingness to learn (high CMs) then the complete acquisition of the revolutionary song had a higher chance to occur, either during the first feeding season or during the second breeding season. Even with high c values, however, revolutions

did not always happen and so, under this set of hypotheses about song learning, revolutions are inherently stochastic events.

Perhaps counterintuitively, song revolutions in population E1 arose only when the third key parameter, feeding season singing probability (P_s), was maintained one order of magnitude lower (0.08) than the breeding season one (0.8). A higher singing probability in the feeding ground increased strongly the probability of an immigrant agent finding itself close enough to a singing resident to store an SR_{E1} song in its memory. Once this occurred, the immigrant agent became more receptive to learning (high CM) and this eventually led it to acquire the SR_{E1} song repertoire, even when the memory conservatism (c) was set to a high value (Figure 3.14).

It is obviously logistically challenging to carry out experimental tests on memory and song learning in the wild. The few playback experiments in which humpback whales were exposed to familiar songs showed contrasting results, ranging from interruption of singing, avoidance and attraction to the playback device (Tyack, 1983; Mobley et al., 1988; Cholewiak, 2008). The only study that tested the playback of an unfamiliar song showed mostly neutral responses and some avoidance by particular individuals (Darling et al., 2012a). In light of the results of the distance + memory learning bias, and relevant literature, I hypothesise a potential scenario in which song types act as 'population markers' (Balaban, 1988), and both song and spatial memory play a synergistic role in the origin of song revolutions. Humpback whale song memory could be part of a parallel memory system as seen in other animals such as dolphins and songbirds. Within this type of parallel system framework spatial and social memory systems interact synergistically with the acoustic memory system (Godard, 1991; Poldrack and Packard, 2003; Bruck, 2013). Humpback whales have been known to perform some of the longest migrations on earth while displaying high site fidelity to their natal breeding/feeding grounds (Herman et al., 2011; Acevedo et al., 2014; Witteveen and Wynne, 2017) and thus are likely to possess a developed long-term spatial memory (Bennett and Tang, 2006; Berbert and Fagan, 2012). This synergic interaction between parallel memory systems might suggest to a hypothetical immigrant whale that finds itself surrounded by individuals singing a different song (i.e. different population marker) that it does not belong to the current area/population. Assuming that

the immigrant whale conservatism towards its population marker (i.e. its song) and the spatial dynamics explored here (one immigrant to many residents) are valid in the wild, then the immigrant whale could display avoidance towards an unfamiliar song (Darling et al., 2012a) or simply not receive enough exposure in order to learn the majority song.

Although the novelty algorithm of model 2 did not produce any song revolutions, the increase in learning (i.e. high conformity mismatch) triggered by the exposure to unfamiliar songs seen in model 3 results could be considered an alternative interpretation of a novelty learning bias. Therefore, assuming that novelty plays a role in humpback whale song learning (Noad et al., 2000) and assuming the spatial dynamics and singing probabilities tested here are realistic, resident whales would have a higher chance of being exposed and therefore learn the novel themes produced the immigrant singer (Garland et al., 2017a). An alternative hypothesis, only partially testable in the current model setting, would assume a whale song memory that spanned over several years, similar to some songbirds and dolphins (Godard, 1991; Bruck, 2013). In this case the directionality of song revolutions (from west to east Australia) would originate from the recognition/recollection by the hypothetical immigrant whale (breeding stock D) of the song sung by the breeding stock E1 as a song already known (an ‘old’ song because it was previously sung by breeding stock D before being transmitted to breeding stock E1 during the prior revolution). Thus the song is not novel and therefore not appealing to be learnt.

In conclusion, in this chapter I used an agent-based modelling approach to explore the potential individual behavioural mechanisms at the origin of the song revolution events recorded in the eastern Australian humpback population. I tested three distinct movement scenarios and a new learning bias. In the first scenario, which did not feature any cognitive bias, song revolutions emerged only when large portions of the two simulated populations overlapped spatially during the feeding season. In the second and third movement scenario the movement of singleton immigrants between the two populations triggered song revolutions only when (i) agents were provided with a song memory, (ii) agents were highly conservative towards their pre-existing memory, (iii) agent density in the feeding ground was high and (iv) feeding season singing probability was low. In the current model setting, a bias toward novelty did not play a role in the

emergence of song revolutions; however, the way high conformity mismatch influenced song learning and revolution could be interpreted as an alternative form of novelty bias. Based on these results, I suggest a general hypothesis that takes into account the individual movement and acoustic behaviour of humpback whales as well as the environmental factors that could alter their distribution and density in the feeding grounds. Prey availability in the Southern Ocean is known to vary both temporally and spatially also due to cyclical large-scale climatic processes, and lower prey availability is likely to increase whales' spatial proximity in the feeding grounds, thereby priming conditions for song revolutions. Considering the unlikeliness of large scale population overlap between the western and eastern Australian populations during the feeding season, the results presented here suggest that song memory and the sense of how well a singer's song fits its current acoustic song-scape could be crucial elements in the individual song learning strategy that leads to population-level song revolutions.

Chapter 4

Inter- and intra-individual variability in humpback whale songs reveals a complex scenario of conformity and individually-distinctive patterns

4.1. Abstract

Recent studies have shown that individually distinctive acoustic signals in animal vocal communication are taxonomically widespread. Until now, the investigation of this type of signal in marine mammals has focused mainly on odontocetes such as bottlenose dolphins, killer and sperm whales. Humpback whales provide an interesting example of a sexually selected signal, a stereotyped vocal display defined as 'song'. Within a population, whales in acoustic contact tend to conform to a common version of the song even if this is constantly evolving. While humpback songs have been studied extensively, little effort has been dedicated to quantify fine-scale conformity, and inter-individual variability has been described in just a few cases, with contradictory results. Here I addressed this gap by quantifying intra- and inter-individual variability at different levels in the song hierarchy across two song type examples: the song sung in eastern Australia in 2002, and the revolutionary song introduced into the same population the following year (2003). I used a robust song similarity analysis method, the Levenshtein Distance, to measure variability in sub-phrases and songs produced by 25 distinct singers. The results presented here reveal a complex scenario in which inter-individual variability is not found across all hierarchical levels of the song structure or even within a single level. While some sub-phrase types displayed high variability, others were homogeneous both within and between individuals. Distinct and consistent individual patterns were found in both sub-phrases and songs, with clear structural differences between the two song types. These results suggest that within the constraints of a highly conformist acoustic system, male humpback whales are able to produce individually distinctive patterns. These idiosyncrasies could function as an advertisement to females to convey individual mate quality analogous to some songbird species.

4.2. Introduction

In animal communication, senders often broadcast signals encoding information about their phenotype to receivers, this can encompass information such as species, local population, age, body size, dominance status and individual identity, to cite just a few examples (Bradbury and Vehrencamp, 2011). In recent years, the study of animal vocal communication has shown how the presence of individually distinctive acoustic signals is more widespread across species than previously thought. Many studies have provided evidence for high inter-individual call variability in birds (Robisson et al., 1993; Charrier et al., 2001; Jouventin and Aubin, 2002; Berg et al., 2011), bats (Arnold and Wilkinson, 2011; Carter et al., 2012), deer (Reby et al., 1998; Vannoni and McElligott, 2008), carnivores (Mathevon et al., 2010; Jansen et al., 2012), primates (Hauser, 1991; Mitani et al., 1996; Fischer et al., 2002; Spillmann et al., 2010; Clay and Zuberbühler, 2011; Leliveld et al., 2011; Bouchet et al., 2012; Miller and Wren Thomas, 2012; Salmi et al., 2014) and other mammals (Soltis et al., 2005; Charlton et al., 2009; Schehka and Zimmermann, 2009; Charlton et al., 2011; Koren and Geffen, 2011). Among marine mammals, bottlenose dolphins (*Tursiop truncatus*) convey their individual identity using signature whistles (Janik and Sayigh, 2013), and there are suggestions that some degree of individual information is also contained in killer whales' (*Orcinus orca*) calls and sperm whales' (*Physeter microcephalus*) codas (Watkins and Schevill, 1977; Nousek et al., 2006; Antunes et al., 2011; Gero et al., 2016b; Oliveira et al., 2016).

Humpback whales provide an interesting example of a sexually selected trait, a complex, stereotyped vocal display defined as 'song' (Payne and McVay, 1971), transmitted across multiple populations over wide geographical scales (Garland et al., 2011). A general finding reported in the literature is that, within a population, whales in acoustic contact show a high degree of individual conformity to a common version of the song even if this is constantly evolving (Winn and Winn, 1978; Payne et al., 1983; Cholewiak et al., 2012). Song content can either change gradually ('song evolution') or more rapidly ('song revolution') over time. Several studies have tracked the gradual addition, deletion and/or modification of units and themes both within breeding seasons and across multiple years (Payne et al., 1983; Payne and Payne, 1985; Cerchio et al.,

2001); songs originating from this gradual change are referred here as ‘evolutionary songs’. Song revolutions result in the rapid and complete replacement of the song sung in a population by the introduction of a novel song, a ‘revolutionary song’, usually produced by an adjacent population. The first documented song revolution occurred in the eastern Australian population, in this occasion the entire song was replaced in less than two years by the introduction of a novel song originating from the western Australian population (Noad et al., 2000).

Variability can be addressed at the multiple levels into which humpback whale songs are hierarchically organised. The fundamental block of this complex display is the shortest continuous sound the ear can perceive: the ‘unit’ (Payne and McVay, 1971). A stereotyped combination of units constitutes a ‘phrase’, which could be considered analogous to bird song phrases. A complex phrase can be subdivided into ‘sub-phrases’ (Cholewiak et al., 2012). The repetition of a phrase forms a ‘theme’(Payne and McVay, 1971; Frumhoff, 1983), and a stereotyped series of themes sequentially sung is defined as a ‘song’ (Payne and McVay, 1971). When analysing a song, the selection of the theme that starts or ends the song is arbitrary, as singers tend to sing in continuous cyclical bouts of several hours, termed ‘song sessions’. A song session contains multiple repetitions of theme sequences, called ‘song cycles’ (Winn and Winn, 1978; Cholewiak et al., 2012). Each unique combination of themes that form a song cycle is defined as a distinct ‘song type’ (Garland et al., 2011).

While humpback song has been studied extensively for more than 40 years, relatively few authors have focused their efforts in understanding inter-individual song variability. Hafner et al. (1979) measured six acoustic parameters of a single unit type (called a ‘cry’ - typically each unit type is named descriptively) produced by six individuals recorded in the Caribbean. The results of a discriminant analysis suggested that features such as the number of inflection points, and unit start frequency, could be used to discriminate among the recorded individuals. However, the individuals were recorded over a period of two years, and thus the authors might have misinterpreted natural song evolution for inter-individual variability (Cholewiak et al., 2012). Subsequent studies of individual variation have mainly focused on investigating how the acoustic features of a subset of song units vary across different individuals. The

results however appear to be contradictory across studies. Frankel (1996) found significant inter-individual differences among six unit types from eleven individuals in Hawaii. In contrast, Cerchio (1993) measured variability within and between individuals on several acoustic parameters without finding significant differences. Similarly, a study conducted off eastern Australia found no consistent acoustic pattern that could help discriminate among different individuals (Macknight et al., 2001). More recently, a study conducted off the coast of Brazil found individual differences in the proportion of use of two structurally different units within a theme from ten different recording sessions likely belonging to be ten distinct individuals (Arraut and Vielliard, 2004). Based on these results, the authors suggested that different individual abilities to learn/compose songs might exist. One robust source of individual variation recorded in multiple studies is the number of phrase repeats per theme (Cerchio, 1993; Arraut and Vielliard, 2004; Cholewiak et al., 2012). Phrase repetition variability for certain themes appears to be related to the behavioural context in which the singer is recorded - alone or escorting a female (Smith, 2009).

Several studies have focused on the acoustic analysis of units and phrases, generating frequency and time domain data that allowed comparisons between different times and/or geographical scales, and, more rarely, individuals (Cerchio et al., 2001; Macknight et al., 2001; Au et al., 2006; Dunlop et al., 2007; Stimpert et al., 2011; Rekdahl et al., 2013). However, in this study I move from directly measuring the acoustic properties of sounds to comparing the way in which they are sequenced together in songs, and measure how that varies within and between individuals. To accomplish this I used an analysis metric commonly used in bioinformatics, the Levenshtein Distance (hereafter termed LD; Levenshtein, 1966), which has proven to be extremely efficient and robust for quantifying similarity in animal vocal sequences (Ranjard and Ross, 2008; Kershenbaum et al., 2012; Kershenbaum and Garland, 2015). The LD has been used in previous studies of humpback whale song to measure the song similarity across different temporal and spatial scales (Helweg et al., 1998; Eriksen et al., 2005; Tougaard and Eriksen, 2006). More recently, this analytical method has been further improved with the introduction of bootstrapping techniques to measure statistically cluster accuracy (Garland et al., 2012; Garland et al., 2013b; Garland et al.,

2015), and unit weighting to account for units' acoustic characteristics when calculating phrase, theme, or song similarity (Garland et al., 2017b).

The study of a sexually selected trait and its inter-/intra-individual variability can provide insights into how trait development and female preference might evolve over evolutionary time scales as well as how trait expression and associated fitness variations might change over individual life histories (Johnstone, 1995; Griffith and Sheldon, 2001). In the past, few studies have looked at humpback whale song inter-individual variability, and those that did usually compared the acoustic properties of a subset of song's units, without finding any conclusive results (Hafner et al., 1979; Cerchio, 1993; Frankel, 1996; Macknight et al., 2001). Here I approach the same issue from an unexplored perspective, looking at the way sub-phrases and themes are sequenced and quantifying the variability within and between individuals using a robust similarity analysis method. This work has three specific goals. (1) As song conformity is one of the most observed (but least measured) characteristics of humpback whale song, I quantify inter-individual variability at different levels in the song hierarchy using two key song type examples: the evolutionary song sung in eastern Australia in 2002, and the revolutionary song introduced into the same population the following year (Rekdahl, 2012). (2) I then use these results to compare the structural variability of the 2002 and 2003 song types in order to generate hypotheses that might contribute to the on-going debate regarding how humpback whale songs are learnt, how they evolve over time and how eventually they can be replaced completely during song revolutions. (3) Finally I analyse the relationship between inter and intra-individual variability across all singers, in both an evolutionary and revolutionary song context, in order to understand how idiosyncratic modifications at different hierarchical song levels might play a role in sexual selection and advertisement.

4.3. Material and Methods

4.3.1. Study Location and Recordings

The songs used in this study were recorded in September and October of 2002 and 2003 at Peregian Beach (26°30´S, 153°07´E), off the east coast of Australia, during the southward migration of the eastern Australian breeding population of humpbacks.

These data were collected as part of a larger collaborative project known as the Humpback Whale Acoustic Research Collaboration (HARC). Songs were recorded using a static array of 5 hydrophones (High Tech HTI-96-MIN) connected via VHS radio transmitters to a shore base station; here the recordings were digitised and stored (sampling frequency = 22050 Hz, 16-bit depth). The hydrophone buoys were located about 700 m apart from each other (approximately1500 m from the coast) and anchored in 18-28 m of water (see Noad et al. (2004) and Dunlop et al. (2007) for further details of construction). Due to the consistent southward migratory pattern shown in this area during the months of September and October (Cato, 1991; Noad et al., 2004; Williamson et al., 2016), I considered song sessions recorded on different days as different individuals. Several hundred hours of song were recorded over the two years' field seasons (172h in 2002; 285h in 2003). From this database I selected recordings that presented all of the following characteristics: (1) a good signal to noise ratio, (2) one recognisable singer present for the entire duration of the song session without interruptions longer than one min, (3) at least two song cycles within the session, and (4) one song session per day to ensure different individual singers were sampled.

4.3.2. Unit, Sub-phrase and Theme Classification

For each recording, two experienced human classifiers (myself and one of three trained research assistants who helped with song transcription) aurally and visually classified each unit present using Adobe Audition 3.0 (window function: Blackman-Harris; FFT size: 4096; 90% window overlap; frequency range inspected: 0 - 5 KHz); this process followed as consistently as possible the previous published classifications of these song types (Dunlop et al., 2007; Miksis-Olds et al., 2008; Smith, 2009; Garland et al., 2012; Rekdahl, 2012; Rekdahl et al., 2013; Allen et al., 2017). Subsequently, units were grouped into sub-phrases (instead of whole phrase types; Figure 4.1) to reflect the high level of complexity present in some phrase types, both in terms of the number of units and unit repertoire. One or more sub-phrases formed a phrase, and repetition of phrases constituted a theme, following the hierarchical structure described in the literature (Payne and McVay, 1971; Cholewiak et al., 2012).

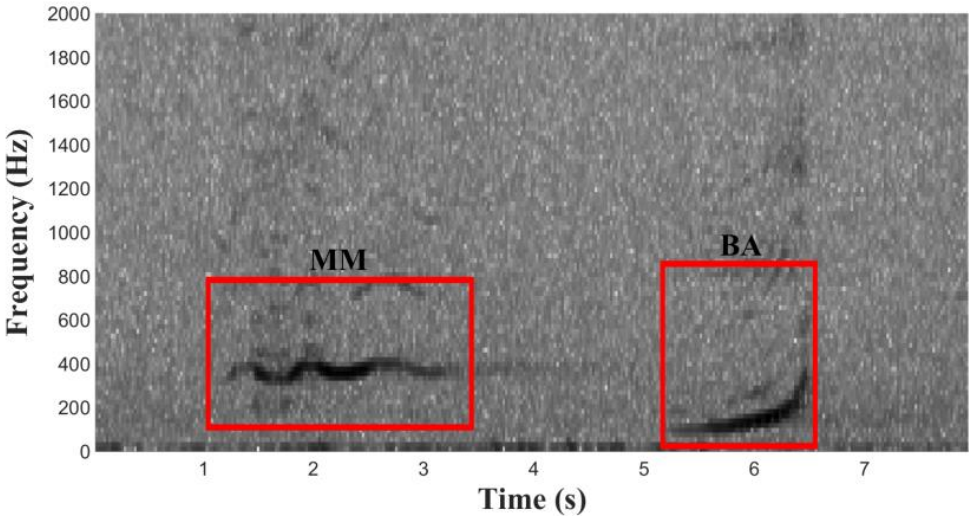


Figure 4.1. Spectrogram of sub-phrase a1; this sub-phrase was formed by two units: a 'modulated-moan' (MM) and a 'bark' (BA). Spectrogram parameters: Hann window, window size: 1024; 50% overlap; generated in Matlab.

4.3.3. Levenshtein Distance (LD) Analysis

Song transcription resulted in sequences (or strings) of units (forming sub-phrases) and sequences of themes (forming songs). Multiple song cycles from the same individual in the same recording constituted a song session. To investigate intra- and inter-individual differences among song cycles, their similarity was quantified using the LD method. The LD calculates the number of edits (substitutions, additions or deletions) needed to transform string *a* into string *b* (Equation 4.1) (Levenshtein, 1966; Kohonen, 1985),

$$LD(a, b) = min(i + d + s), \qquad \text{(Equation 4.1)}$$

where string *a* is transformed into string *b* using the minimum required number of insertions (*i*), deletions (*d*) and substitutions (*s*). The LD output of Equation 1 is then standardised for each pair of strings by dividing by the length of the longer string, giving a quantity that has been termed the Levenshtein Similarity Index, or LSI (Garland et al., 2012). The LSI allows comparison among many different pairs of strings with varying lengths. In this study I carried out the LD method at two hierarchical levels – first, using using strings of units to look at sub-phrase composition - similar to Garland et al. (2017b) and Murray et al. (2018) – and secondly using strings

of themes to evaluate song composition; in both cases I used the routines developed by Garland et al. (2012); 2017b. If multiple analysed strings belong to a set (for example, multiple song cycles or multiple instances of a given sub-phrase from the same individual in the same song session), a helpful step is to identify a median or representative string for the set. The string with the highest similarity to all the other strings in its set is designated the median string (Kohonen, 1985) and can be used to compare different sets of strings. Here I calculated a set median per individual singer for 1) each sub-phrase and 2) the overall theme string, such that I had, for each individual, a median sub-phrase string for each sub-phrase used, and a median theme string for the overall song.

All LD analyses were run in R (R Core Team, 2016) using custom written code provided by Ellen Garland (Garland et al., 2017b; available at https://github.com/ellengarland/leven). The primary analysis output is an LSI matrix that includes all of the pairwise string similarity coefficients for the set of provided strings. The LSI matrices generated in this study were visualised both using hierarchical cluster analysis (using average-linkage clustering), and assigning different colours to different levels (percentages) of similarity within a plotted matrix (the latter type of plot was produced in Matlab).

I assessed the statistical uncertainty of the clusters using the *pvclust* package in R (Suzuki and Shimodaira, 2006; Garland et al., 2012; Garland et al., 2017a; Garland et al., 2017b). I performed a bootstrapping analysis (1000 times) and calculated *p*-values for each cluster in my results. The *pvclust* package provides approximately unbiased *p*-values (AU, significance for $p > 95\%$) using multi-scale bootstrap resampling as well as bootstrap probability values (BP, significance for $p > 70\%$). Furthermore, each time a dendrogram was produced during the analysis, I measured how well it preserved the pairwise distances between the similarity matrix data points using the Cophenetic Correlation Coefficient (CCC) (Sokal and Rohlf, 1962). Dendrograms in which CCC values were above 0.8 indicated a good representation of the data (Garland et al., 2017a).

4.3.4. Quantifying Individual Idiosyncrasies

Finally, I investigated individual patterns at the sub-phrase and song levels; in order to quantify the variability within and between individuals I analysed LSI matrices using Mantel tests. The Mantel test is widely used in biology and ecology to investigate the correlation (and its significance) between matrices containing pairwise distances (Mantel, 1967). I measured the correlation between the LSI matrix and an individual binary matrix (IBM) where 1 represented a pair of sub-phrases or songs that were produced by the same individual and 0 a pair of sub-phrases/songs produced by different individuals. Thus a significant positive correlation would indicate that songs made by the same individual were significantly more similar to each other than songs made by different individuals. The null hypothesis was that there was no significant correlation between the sub-phrase or song LSI matrices and the corresponding IBM matrices, indicating that the variability within and between individuals is equivalent. I performed each Mantel test in R (R Core Team, 2016) using the package *vegan* (Oksanen et al., 2017) with the Pearson correlation method and 999 permutations. A simplified example is visualised in Figure 4.2 below.

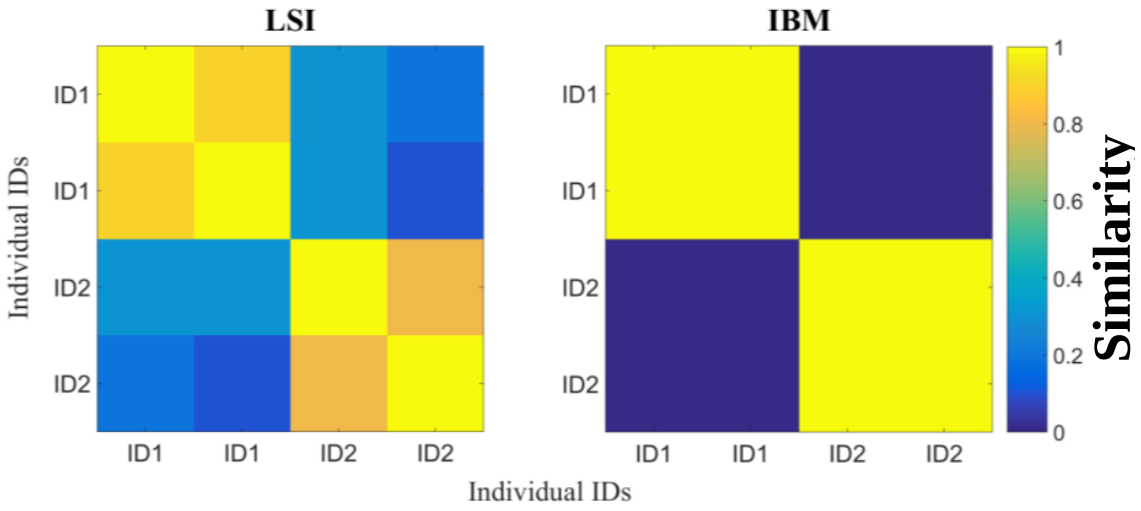


Figure 4.2. A hypothetical example of the correlation performed between an LSI matrix and an IBM matrix. The LSI matrix shows the similarity scores between the songs of two individuals (ID1 and ID2) each producing two strings (ID1 rows/columns 1&2; ID2 rows/columns 3&4). The IBM matrix takes the value 1 where the song pair is produced by the same individual and 0 otherwise.

4.4. Results

The song transcription process resulted in data from 25 singers (12 from 2002, 13 from 2003), with over 32 hours of songs, 261 song cycles and 42,613 units being analysed (Table 4.1).

Table 4.1. Summary of song transcriptions from eastern Australia 2002 (light shading) and 2003 (dark shading).

Whale ID	*Date (yy/mm/dd)*	*Start Time (hh:mm:ss)*	*# Units*	*Transcription duration (hh:mm:ss)*	*# Song cycles*
13	02/09/21	06:03:11	3238	02:06:10	14
14	02/09/25	07:43:31	2499	01:53:21	10
19	02/09/26	06:02:20	2818	02:03:25	11
23	02/09/30	14:38:43	1283	00:57:55	5
15	02/10/03	12:34:35	1670	01:12:59	6
24	02/10/05	06:48:00	2676	01:55:20	14
21	02/10/08	14:20:04	4158	02:56:03	17
22	02/10/12	16:59:09	2131	01:29:50	7
25	02/10/18	15:06:28	2828	02:01:13	14
26	02/10/21	17:02:39	1660	01:14:30	7
20	02/10/22	11:19:52	3299	02:33:42	19
16	02/10/23	13:53:45	1282	00:58:56	3
1	03/09/18	12:30:33	669	00:30:41	5
2	03/09/24	16:52:47	1200	00:47:33	10
3	03/09/26	13:03:59	695	00:29:00	9
27	03/09/30	Missing	930	00:35:10	2
4	03/10/03	05:36:21	770	00:36:17	7
5	03/10/09	19:59:15	1700	01:23:38	22
17	03/10/10	19:46:07	898	00:35:42	4
8	03/10/15	15:09:15	787	00:46:13	12
12	03/10/22	17:53:18	2167	01:50:11	23
9	03/10/23	11:49:23	495	00:28:45	7
10	03/10/24	16:01:41	1301	01:21:02	9
7	03/10/25	06:41:25	265	00:20:26	4
6	03/10/26	23:08:36	1194	01:34:08	19
25	**TOTAL**		**42613**	**32:42:13**	**261**

The song session of whale ID 27 was recorded in 2003 (3rd September 2003) but included only themes from the 2002 song type – this whale had not made the switch to the revolutionary 2003 song at the time of recording. For this reason, whale ID 27 was

included in the 2002 dataset for analysis. The final dataset comprised 13 singers for the 2002 song type and 12 from the 2003 song type. I analysed the song sequences at two different hierarchical levels (sub-phrase and song level) in order to understand the different degrees of individual variability present in each.

4.4.1. Inter-individual Variation at the Sub-phrase Level

The 2002 and 2003 song type datasets were analysed separately and then compared for any consistent patterns of similarity. A total of 5599 sub-phrases were transcribed for the 2002 song type, grouped into 12 sub-phrase types (Figure 4.3A), while the 2003 dataset comprised 3557 sub-phrases, organised into 7 sub-phrase types (Figure 4.3B). These two sub-phrase datasets were then used in the LD analysis to evaluate both the degree of similarity across different sub-phrase types and the amount of individual variability within each sub-phrase type. Due to the large number of sub-phrases in this part of the analysis, after the LD analysis was conducted to ensure consistent classification of all sub-phrases, I calculated the set median sub-phrase types for each individual for further comparison. Results are grouped below following the three most distinct patterns that became apparent while investigating sub-phrase variability between individuals.

4.4.1.1. Sub-phrases Showing Low Variability between Individuals

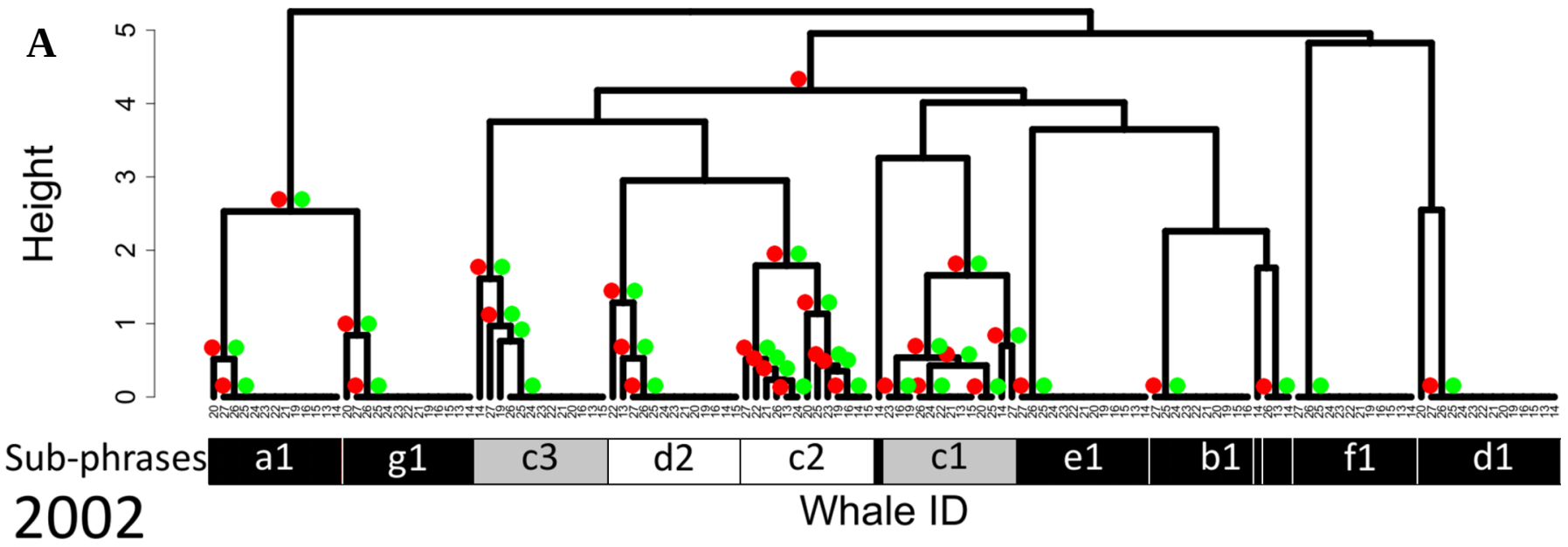
In the evolutionary song of 2002 both sub-phrases a1 and g1 comprised three to four ‘croak’ (CRK) repeats; they differed in the initial unit of the sequence, a modulated-moan (MM) for a1 and a ‘bellows’ (BLW) for g1 (Figure A4.1 & Table A4.1). Inter-individual variability was extremely low in these sub-phrases, with the exception of individual ID20, who consistently sang both sub-phrases with only three croaks (black shading; Figure 4.3A). Similarly, sub-phrases f1, d1, b1 and e1 presented low inter-individual variability. Sub-phrases f1 and d1 were distinctive (black shading; Figure 4.3A) because the units they were composed of – ‘long-bark’ (LBA) & ‘bark’ (BA) for f1 and ‘siren’ (SI) and ‘mini-siren’ (MSI) for d1 – were not found in any other sub-phrase type. Sub-phrase e1 showed complete conformity across individuals while in sub-phrase b1 three individuals made a slight substitution in the initial unit - a ‘modulated-moan’ (MM) - instead of an ‘ascending-moan’ (AM). Finally, two

additional sub-phrases, i1 and h1, were identified only on one occasion, sung by whale ID14. Both sub-phrases were composed by unique units such as the ‘eee’ unit (E), ‘bird-whistles’ (BW) and ‘modulated-whoops’ (MW), which were not present in any other sub-phrases of the 2002 song type.

In the ‘revolutionary’ song of 2003, sub-phrases j1, k1 and l1 were sequential in the song and their rendition was completely consistent across all singers (black shading; Figure 4.3B). All three sub-phrases were formed by two units, the first unit being a ‘modulated-moan’ (MM) while the second unit was either a ‘bark’ (BA) for j1, a ‘long-bark’ (LBA) for k1 or a ‘long-growl’ (LGO) for l1.

4.4.1.2. Sub-phrases Showing Individual Variability in the Number of Repetitions of the Same Unit

In the 2002 song, sub-phrase c1 displayed some inter-individual variability, predominately in the number of ‘grunt’ (GR) repeats (grey shading; Figure 4.3A; Table A4.1). Similarly, individual variability in sub-phrase c3 originated from the different number of repetitions of the ‘trumpet’ unit (TR). In the 2003 dataset, sub-phrases m1 and n1 displayed different repetitions of ‘grunts’ (GR) and ‘ratchets’ (RA) respectively (grey shading; Figure 4.3B). Sub-phrases o1a and o1b were sung sequentially and were characterised by the same initial starting units: a ‘high-modulated-moan’ (HMM) and ‘high-shriek’ (HSH) (Figure A4.2 & Table A4.2), followed by either two to four ‘high-squeaks’ (HSQ; sub-phrase o1a), or several repeated ‘bird-whistles’ (BW; sub-phrase o1b).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Sub-phrases
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g1
c3
d2
c2
c1
e1
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f1
d1
2002
Whale ID

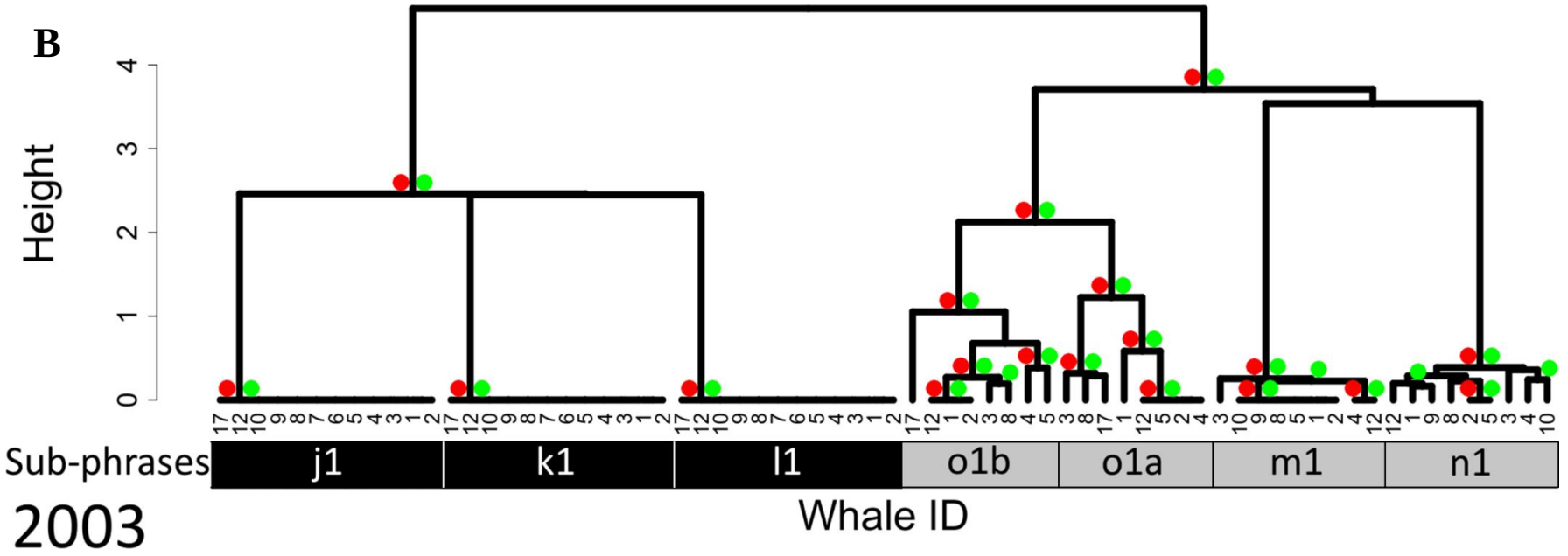


Figure 4.3. Dendrogram of bootstrapped (1,000) dissimilarity matrices of individuals' median strings for each sub-phrase type in A) 2002 and B) 2003. Multiscale bootstrap resampling (AU, left, red dot indicates $P > 95\%$) and normal bootstrap probabilities (right, green dot indicates $P > 70\%$) are shown. Branches with high AU values are strongly supported by the data. Whale IDs are reported at the base of the dendrogram, they are represented multiple times – once for each sub-phrase. The three patterns of sub-phrase variability between individuals are shown with different colour shadings: black, low variability; grey, variability in the number of repetitions of the same unit; white, variability in the arrangement of the same units. The CCC scores calculated for the 2002 and 2003 dendrograms are 0.98 and 0.99, both indicating excellent data representation.

4.4.1.3. Sub-phrases Showing Individual Variability in the Arrangement of the Same Units

The inter-individual variability displayed in sub-phrases c2 and d2 in the 2002 evolutionary song was mainly due to variable arrangements of the same unit types (Table A4.1). More specifically, the c2 cluster displayed a larger number of branches compared to other 2002 sub-phrases, indicating a relatively high degree of inter-individual variability (white shading; Figure 4.3A). In addition, the c2 cluster was characterised by the presence of two sub-clusters splitting the pool of singers almost in half (6 vs 7); these two sub-clusters represented what I considered as two concurrent versions of sub-phrase c2 (Figure 4.4). This was an artefact of the median string computation as all singers generally sang both versions of this sub-phrase one after the other. These two concurrent versions of c2 were formed almost entirely by the same pool of units - excluding 'descending cries' (DC) and 'short-shrieks' (SSH) occasionally present in c2b - and therefore were initially labelled under the same sub-phrase label.

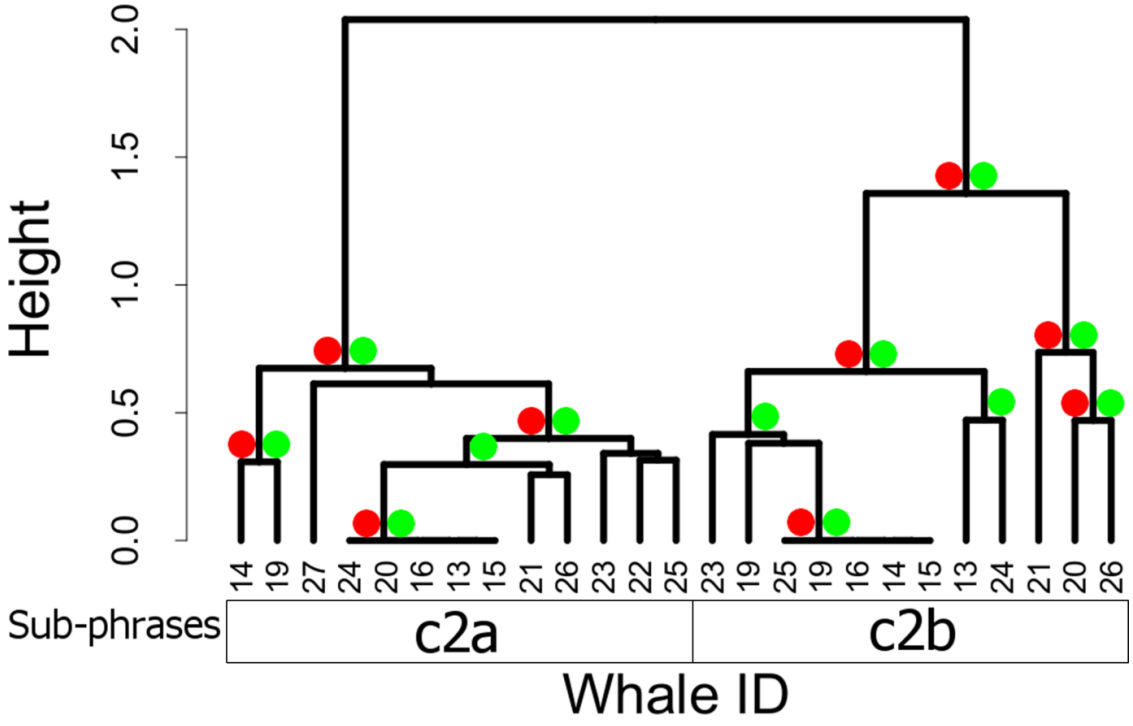


Figure 4.4. Dendrogram of bootstrapped (1,000) dissimilarity matrix of individuals' median strings for sub-phrase types c2a and c2b (2002 song). Multiscale bootstrap resampling (AU, left, red dot indicates $P > 95\%$) and normal bootstrap probabilities (right, green dot indicates $P > 70\%$) are shown.

Branches with high AU values are strongly supported by the data. Whale IDs are reported at the base of the dendrogram. CCC score calculated for this dendrogram is 0.93 indicating excellent data representation.

The LDI analysis suggested that a classification into two different sub-phrase types (Cholewiak et al., 2012), c2a and c2b (Figure 4.4), would be more appropriate in this case. Sub-phrase c2b could also be identified as a 'transitional' phrase due to the fact that it incorporated units of the preceding sub-phrase (c2a) with units of the following (d2) (Payne and Payne, 1985). Nevertheless, even if c2a and c2b were to be considered separate sub-phrases, they both displayed a higher level of variability between individuals compared to the highly consistent sub-phrase types that comprised the majority of the 2002 song (Figure 4.3A). In the revolutionary song of 2003 there were no examples of sub-phrase types in which the inter-individual variability consistently originated from different arrangements of the same pool of units.

4.4.2. Inter-individual Variation at the Song level

The dataset at the song level comprised 261 song cycles, 129 from 13 singers in 2002 and 132 from 12 singers in 2003 (Table 4.2).

4.4.2.1. Theme Composition

Each theme was formed by a combination of sub-phrases repeated multiple times. Themes could be both formed by a single sub-phrase and by combinations of multiple sub-phrases. Generally, themes from the 2002 song type included more numerous and variable sub-phrase combinations compared to the 2003 song type (Table 4.2).

Table 4.2. Theme list for the 2002 and 2003 song types; each theme was formed by a sub-phrase combination. When possible, the correspondent theme labels found in the literature were reported (Garland, 2011; Garland et al., 2012; Garland et al., 2013b; Allen et al., 2017; Garland et al., 2017a). The most commonly used themes are represented by light shading. Themes found in less than 15 % of song cycles and used by less than half of the singer in the sample were considered rare (dark shading).

2002					**2003**				
Sub-phrase combination	***Theme***	***Literature***	***# Song cycles***	***# Individuals***	***Sub-phrase combination***	***Theme***	***Literature***	***# Song cycles***	***# Individuals***
a1	A1	30a	129/129	13/13	*j1*	J1	31	132/132	12/12
b1	B1	/	106/129	13/13	*k1*	K1	33	118/132	12/12
c1, c1, c3	C1a	25a	98/129	13/13	*l1*	L1	34	71/132	12/12
c1, c1, c2	C1b	25b	115/129	11/13	*m1*	M1	32	40/132	9/12
c1, c3	C1c	/	45/129	8/13	*n1*	N1	36	80/132	9/12
d1, d2	D1a	/	103/129	11/13	*o1a*	O1a	37a	45/132	8/12
d1, d2	D1b	26a &b	129/129	13/13	*o1b*	O1b	37b	45/132	8/12
d1, e1, e1, e1	D1c	28a	129/129	13/13					
f1, b1, b1, b1	F1b	28b	94/129	10/13					
g1	G1	29	127/129	13/13					
c1, c2	C1d	/	13/129	4/13					
f1	F1	/	8/129	2/13					
f1, e1, e1, e1	F1a	/	12/129	2/13					
f1, b1, b1	F1c		16/129	3/13					
e1	E1	/	9/129	5/13					
i1	I1	23	1/129	1/13					
h1	H1	24	1/129	1/13					

In 2002, ten themes were consistently sung by the majority of sampled individuals (Table 4.2; light shading) while seven other themes – mostly variations of the more common ones – were found in less than 15 % of all song cycles and sung by less than half of the sampled singers (Table 4.2; dark shading). Whale ID14 was the only singer that produced themes I1 and H1 in this sample. This dichotomy between more common and rarer themes was absent in the 2003 songs - most singers produced all 2003 themes.

4.4.2.2. Theme Usage

The 2002 theme repertoire was larger than the one present a year later in the revolutionary song of 2003 (Table 4.2). However, this difference became even more pronounced when examining the number of unique themes used in each song cycle by singers in both years (Figure 4.5).

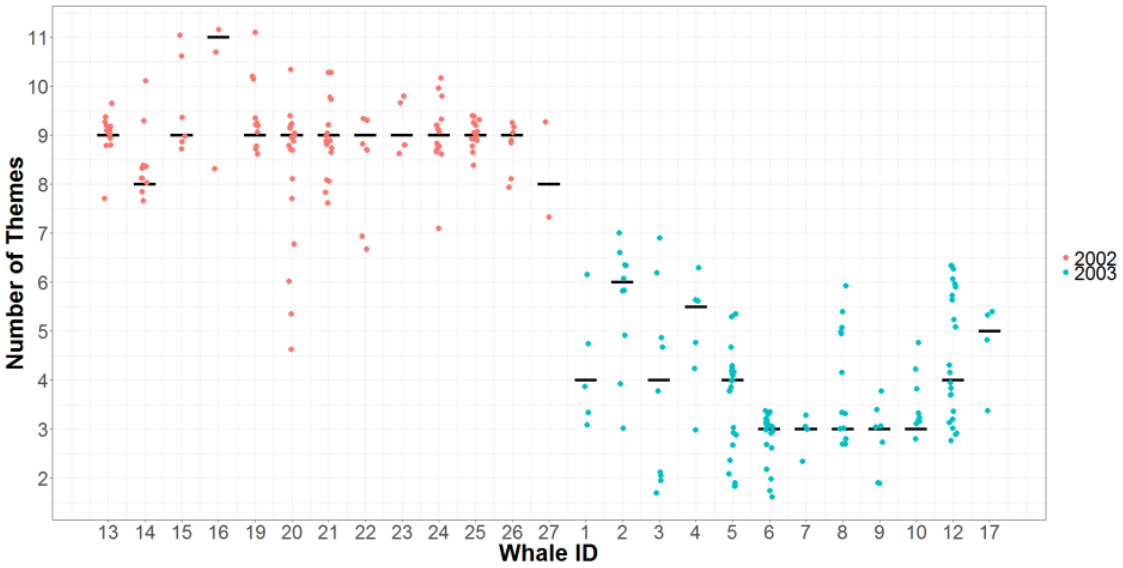


Figure 4.5. Number of unique themes used in each song by each individual in 2002 (red dots) and 2003 (blue dots). The lines represent the median of each individual's set of songs. Data points, each representing one song cycle, were jittered to aid visualisation.

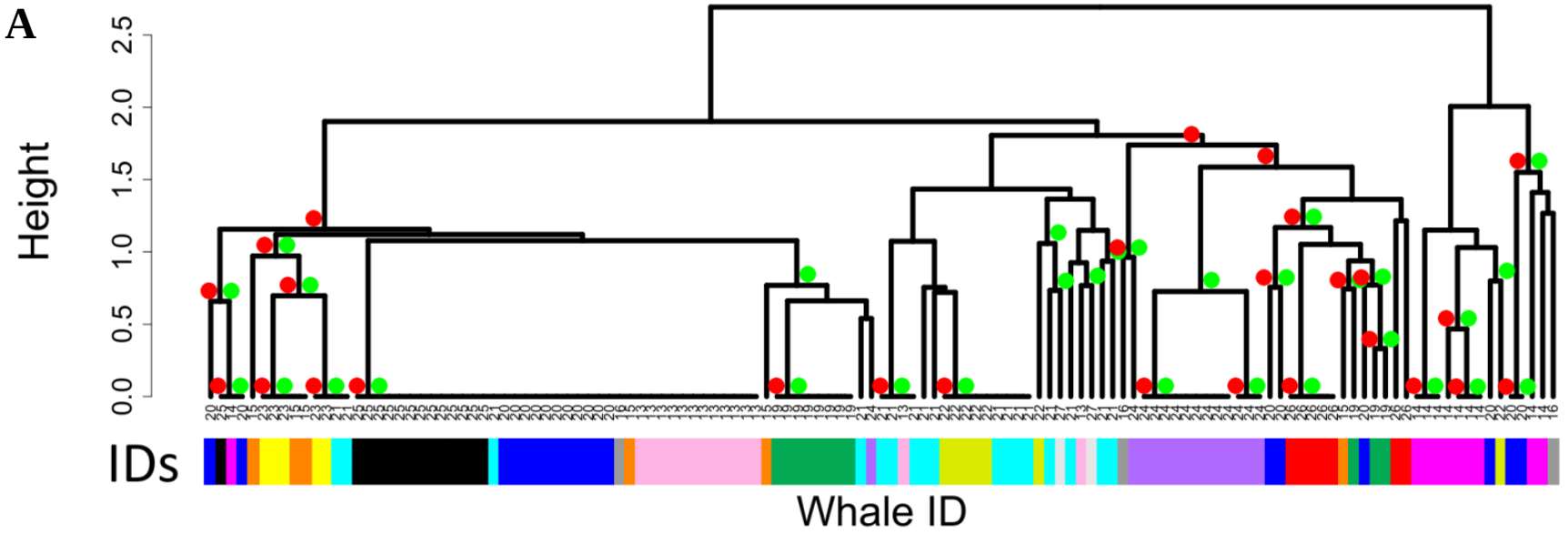
In 2002 10 out of 13 individuals used a median of nine themes in each cycle, and none had a median lower than 8, while 9 of 12 whales in 2003 produced a median of 3 or 4 themes per song, with none having a median greater than 6. While there was considerable variability within individuals in the number of themes in each song cycle,

only 7 of the 129 2002 song cycles analysed fell within the range of the 2003 songs on this measure. This confirmed that the songs produced within a single song session by the same individual were not exact copies of one another, but also that there was a marked change in the number of themes used before and after the revolution event.

4.4.2.3. Song Similarity

Smith (2009) observed that the number of times a phrase was sung within certain themes varied across behavioural contexts – alone or escorting a female for example. Therefore I controlled for this potentially confounding factor by conducting the LD similarity analysis on theme sequences (i.e. songs) with and without within-theme phrase repeats. For example, if a song were to be composed by themes sequenced - A1, A1, B1, B1, B1, B1, C1 – I would have conducted the LD analysis both on the original sequence and on the one in which phrase repetition was removed – A1, B1, C1.

All song strings of the 2002 dataset were used in this LD analysis (no medians). Clusters of similar songs produced by the same individual were present when phrase repetitions were removed from the song sequences (Figure 4.6A). For certain individuals – such as ID25, 20 and 13 (corresponding respectively to black, blue and pink in Figure 4.6A) – inter-individual variability was entirely absent; generally, they produced the same themes following the same sequence. However, there are other cases – such as ID19, 24 and 14 (corresponding respectively to green, purple and fuchsia in Figure 4.6A) – where singers produced theme sequences that were different from all the other individuals, forming individual sub-clusters (Figure 4.6A).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Whale ID

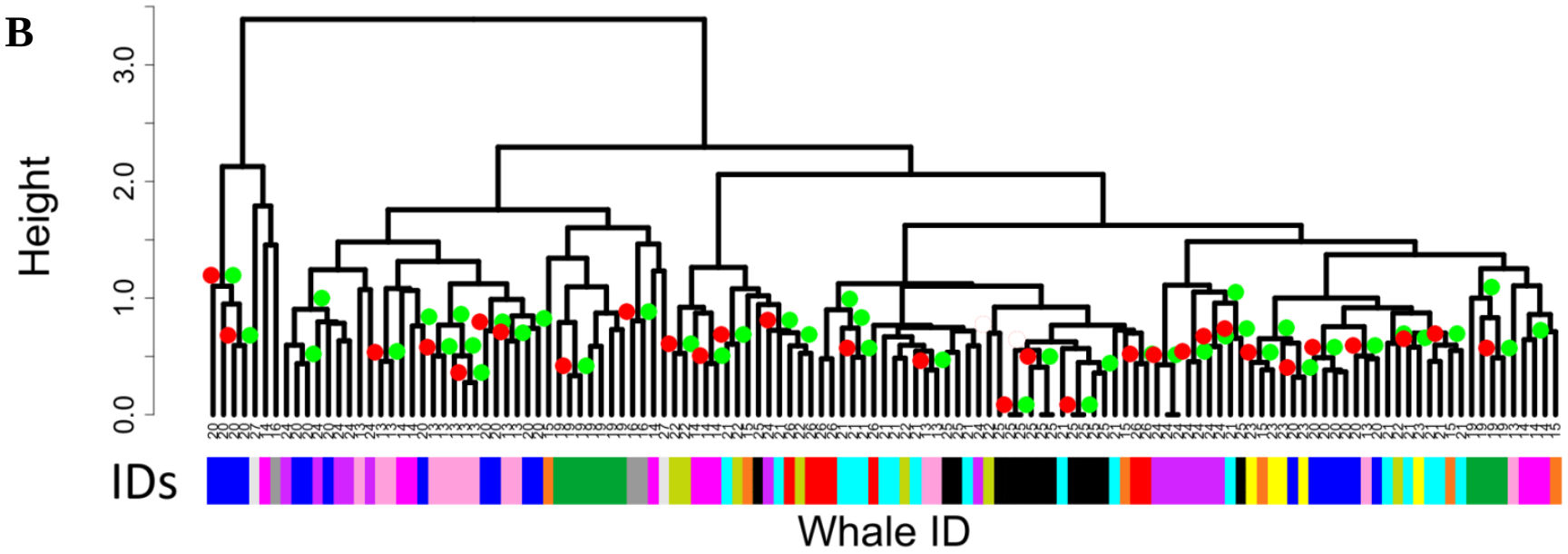
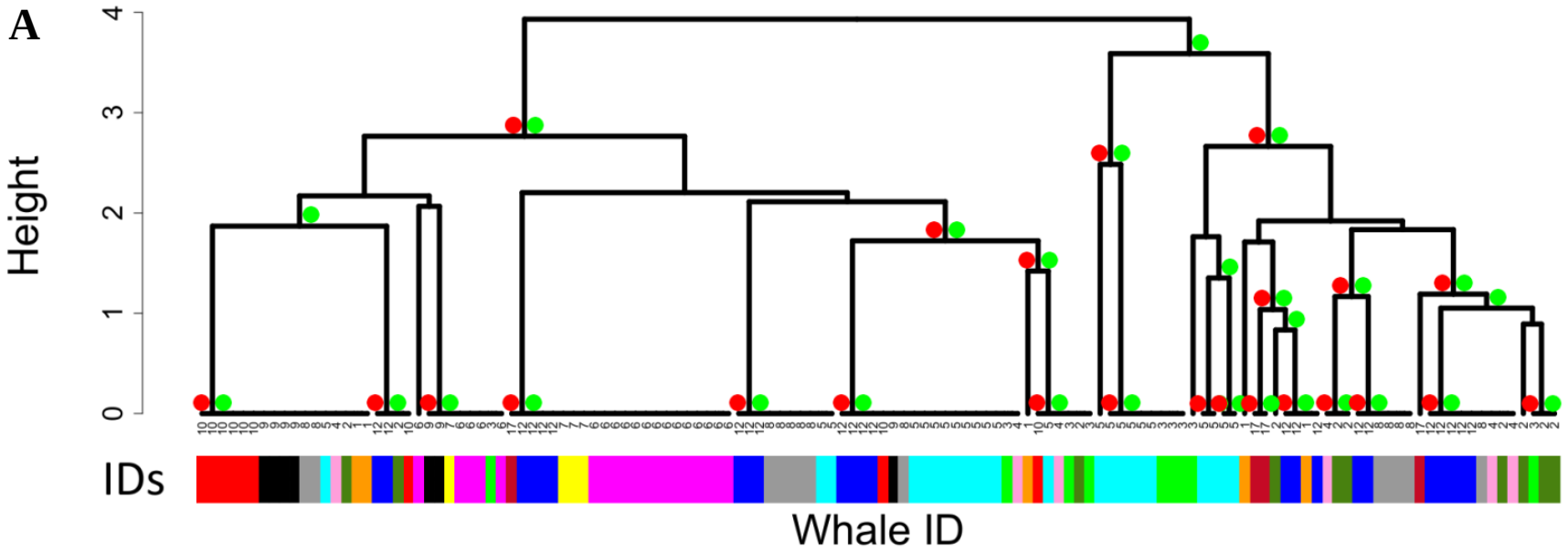


Figure 4.6. Dendrogram of bootstrapped (1,000) dissimilarity matrices of individuals' songs in 2002 without (A) and with (B) within-theme phrase repetition. Multiscale bootstrap resampling (AU, left, red dot indicates $P > 95\%$) and normal bootstrap probabilities (right, green dot indicates $P > 70\%$) are shown. Branches with high AU values are strongly supported by the data. Whale IDs are reported at the base of the dendrogram and with corresponding colours to emphasize the presence of individual clusters. CCC score calculated for these dendrograms are 0.84 (A) and 0.76 (B) indicating respectively good and poor data representation.

Obviously there was an increase in variability both within and between individuals once phrase repetitions within themes were considered (Figure 4.6B). The mean LSI similarity score when repetitions within themes were removed was 0.755 (*SD* = 0.147); this value decreased to 0.579 (*SD* = 0.158) with the repetitions, a decrease in similarity that corresponded to an increase in diversity. This difference was readily visible by comparing the respective dendrograms (Figure 4.6A and B). It was common to have no song variability between certain individuals when repetitions were removed (Figure 4.6A; the cluster formed by ID25, 20 and 13 is a good example of this); conversely, when phrase repetitions within themes were accounted for, identical song sequences were extremely rare, with the exception of four instances (ID25 and ID 24, corresponding respectively to black and purple in Figure 4.6B).

In the 2003 songs, the sequences without phrase repetition were clustered in two major groups (Figure 4.7A). The larger cluster (on the left in Figure 4.7A) contained song sequences with 2-3 themes (usually J1, K1 and L1/M1) while the cluster on the right included songs with a larger number of themes. Excluding four singers – ID6, 7, 9 and 10 (Figure 4.7A) – all individuals were found at least once in both clusters, indicating that across all songs, most of the whales sang both a shorter and a longer version of the 2003 revolutionary song type. While it was very common to have different singers singing identical song sequences when repetitions were not considered (Figure 4.7A), the individual sub-clusters observed in the 2002 data (for example whales ID19, 24 and 14 in Figure 4.6A) were absent in the 2003 songs – in 2003, whales sang theme sequences consistently with much less variation between individuals.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Whale ID

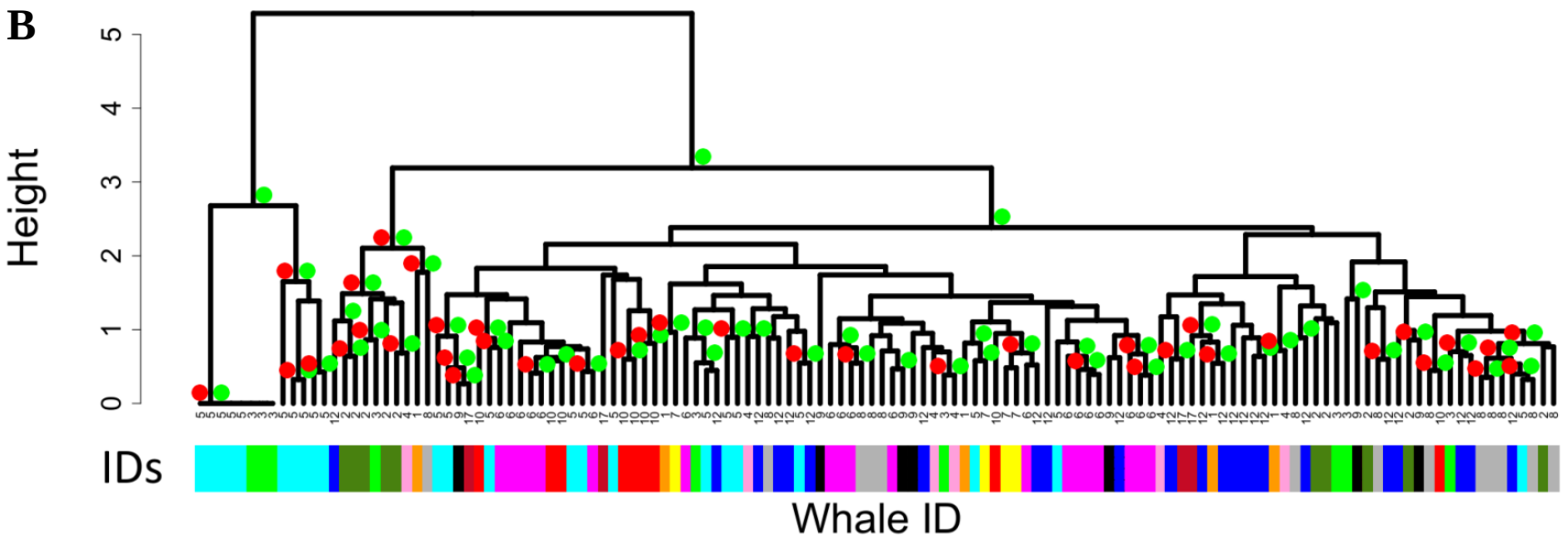

Figure 4.7. Dendrogram of bootstrapped (1,000) dissimilarity matrices of individuals' songs in 2003 without (A) and with (B) within-theme phrase repetition. Multiscale bootstrap resampling (AU, left, red dot indicates $P > 95\%$) and normal bootstrap probabilities (right, green dot indicates $P > 70\%$) are shown. Branches with high AU values are strongly supported by the data. Whale IDs are reported at the base of the dendrogram and with corresponding colours to emphasize the presence of individual clusters. CCC score calculated for these dendrograms are 0.91 (a) and 0.85 (b) indicating excellent data representation.

As expected, the mean LSI similarity scores decreased from 0.563 (*SD* = 0.211; Figure 4.7A), when repetitions were not counted, to 0.407 (*SD* = 0.221; Figure 4.7B) when they were, indicating that a portion of song variability within and between individuals was due to varying numbers of phrase repeats.

4.4.2.4. Median Song Similarity Between Individuals

The analysis of individual median theme sequences confirmed some of the results seen in the previous sections where all song cycles were taken into account. Individual median theme sequences were much longer in 2002 (minimum of eight themes) compared to 2003 (minimum of three themes; Figure 4.8). Moreover, based on theme sequence length, individuals in 2003 could be subdivided into two groups displaying consistently short (ID1, 6, 7, 8, 9 and 10) and long (ID2, 3, 4, 5, 12 and 17) median songs (Figure 4.8, right panel).

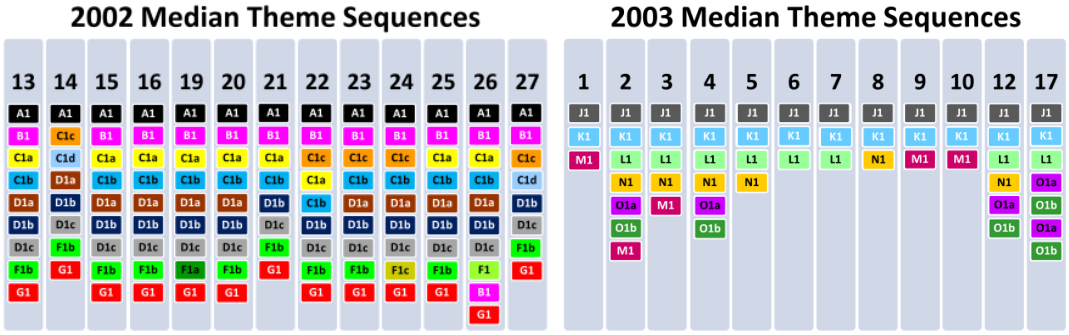

Figure 4.8. Individual median song sequences (without phrase repetitions within theme) for 2002 (left) and 2003 (right) song types. Whale ID's are listed in row 1.

The analysis of which themes formed each individual median song (Figure 4.8) and the similarity among median theme sequences (Figure 4.9) provided new information. Although individual variations were present in individual median theme sequences from 2002 (for example, ID24 sang F1c instead of F1b; Figure 4.8), singers displayed a higher song conformity overall compared to 2003 – for example, the highest dissimilarity level in 2002 was 0.8 (no phrase repetition; Figure 4.9B) while in 2003 it increased to 1.2 (Figure 4.9D). Moreover, when phrase repetition was removed from the 2003 median theme sequences, four clusters of individuals resulted from the LD

similarity analysis (Figure 4.9D). The first cluster included ID6, 7, 8 which produced predominantly only three themes (J1, K1, L1; whale ID8 had N1 instead of L1; Figure 4.9D). The second cluster was formed by singers ID3 and 5 which, compared to the previous group, added to their median song themes N1 and M1. The third group of individuals (ID1, 9, 10) was characterised by the theme transition K1to M1, which was not recorded in other median theme sequences. Finally, the fourth group comprised four singers (ID2, 4, 12, 17) that produced the longest median theme sequences, which included themes O1a and O1b (Figure 4.9D). It is important to note that some individuals present in the clusters with shorter median songs also produced, even if rarely, longer versions of the 2003 song (Figure 4.7A); therefore the median theme sequence results here must be interpreted with this caveat. Overall, singers that had very similar theme sequences when phrase repetitions were included (Figure 4.9A and C) did not seem to maintain the same level of similarity once the repetitions were removed (Figure 4.9B & D) indicating that phrase repetition played an important role in defining the structural characteristics of a song.

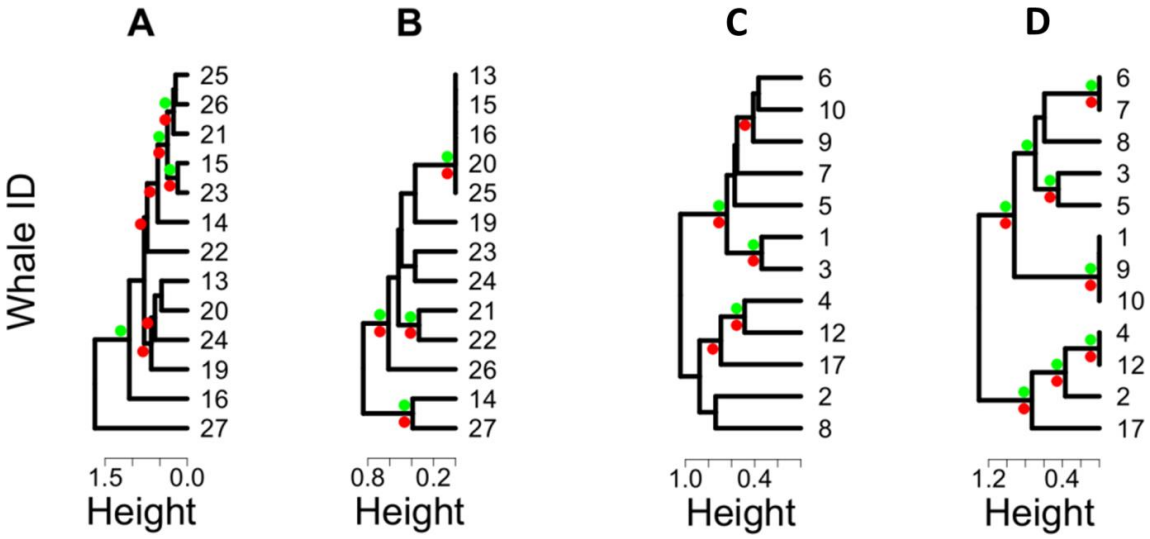

Figure 4.9. Dendrogram of bootstrapped (1,000) dissimilarity matrices of individuals' median songs in 2002 - 2003 with (A, C) and without (B, D) within-theme phrase repetition. Multiscale bootstrap resampling (AU, left, red dot indicates $P > 95\%$) and normal bootstrap probabilities (right, green dot indicates $P > 70\%$) are shown. Branches with high AU values are strongly supported by the data. Whale IDs are reported on the right side of the dendrogram. CCC score calculated for these dendrograms are 0.95 (A), 0.98 (B), 0.85 (C) and 0.93 (D) indicating excellent data representation.

4.4.3. Individual Idiosyncrasies at the Sub-phrase Level

I computed for each sub-phrase type an LSI matrix using all the strings available for each individual (no medians); its size corresponded to the sum of the times each individual produced that specific sub-phrase. Subsequently, these different sample sizes were combined to build the IBM matrix that was then compared to the corresponding LSI matrix using the Mantel test. Four qualitative categories arose from this analysis (Figure 4.10). Category A was represented by sub-phrases that showed complete conformity across all individuals (j1, k1 and l1). A clear example is j1 (Figure 4.10A), sung with complete consistency by all 12 singers, more than 1200 times in total. Due to this complete lack variation, it was not possible to carry out Mantel tests for these sub-phrases (Table 4.3). Category B showed widespread sub-phrase variability across all individuals (Figure 4.10B), with no particular pattern present. This led to low correlation scores in the Mantel test (Table 4.3). For example, sub-phrase o1a presented the same level of variability both within and between individuals (Figure 4.10B). In category C conformity in sub-phrases such as f1 and g1 was high across all repetitions of the sub-phrase by all individuals except one (ID20). This whale consistently sang a slightly modified version of the common sub-phrases. For example, he sang sub-phrase f1 with a ‘long-bark’ (LBA) followed by a ‘mini-siren’ (MSI) instead of a ‘bark’ (BA) (Figure 4.10C; Table A4.1). Sub-phrase types in which these individual modifications occurred presented higher, and statistically significant, Mantel correlation scores ($r \sim 0.150$, all $p = 0.018$, Table 4.3).

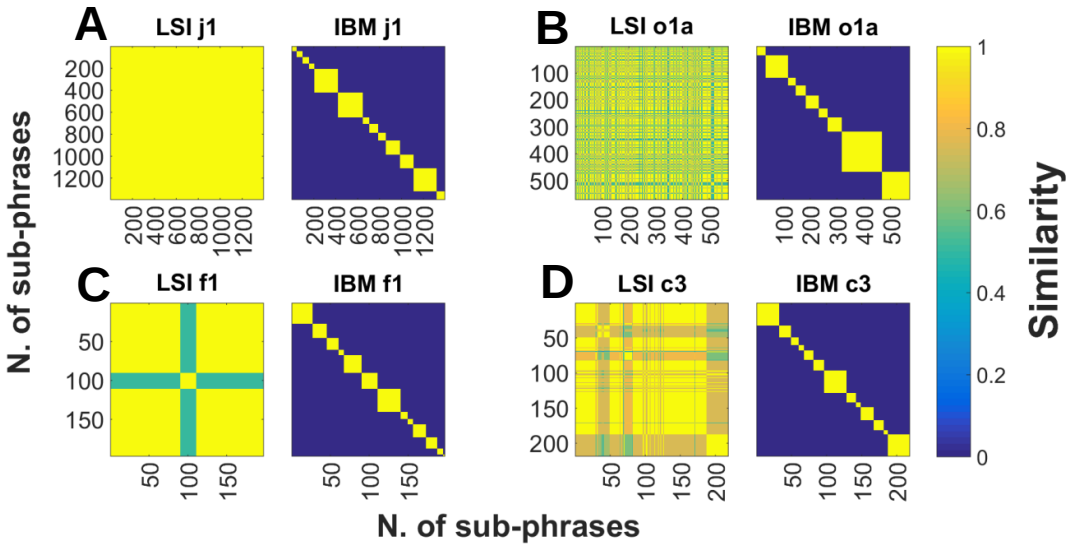

Figure 4.10. Four examples (A: j1; B: o1a; C: f1; D: c3) representative of the four categories of sub-phrase variation within and between individuals found in the analysis. In each example, the correlation between the sub-phrase LSI matrix (left) and its correspondent IBM matrix (right) is calculated. Each yellow square in the IBM matrices represents one individual; its size indicates its sample size (i.e. number of times the sub-phrase was recorded). In a scenario of complete convergence (i.e. LSI matrix in A) all individuals display maximum similarity scores, whereas in a scenario of complete individuality the LSI and IBM matrices would be identical.

Finally, category D sub-phrases such as c3, c2a and c2b were instances in which multiple individuals had idiosyncratic production. For example, three individuals consistently sang three different versions of the common c3 sub-phrase, which is typically formed by an 'ascending-moan' (AM) and three 'trumpets' (TR). While ID14 omitted the initial 'ascending-moan' (AM), ID19 and ID27 consistently performed the sub-phrase with different numbers of 'trumpets' (TR) (Figure 4.10D; Table A4.1). The Mantel correlation for sub-phrase c3 was the highest among all sub-phrase types for both songs (r = 0.224, p = 0.018; Table 4.3). The Mantel tests carried out on this category of sub-phrase types allowed us to reject the null hypothesis that LSI and IBM matrices were unrelated, indicating a higher similarity within rather than between individuals.

Table 4.3. Mantel correlation coefficients and their corresponding *p*-values for all sub-phrase types of 2002 (light shading) and 2003 song (dark shading). Significant correlation coefficients are shown in bold. Due to the large number of statistical tests, all *p*-values were adjusted using a Bonferroni correction.

Song type	*Sub-phrases*	*LSI Matrix size*	*Category*	*Mantel Correlation r*	*p-value*
2002	a1	1408 x 1408	**B**	**0.020**	**0.018**
2002	b1	749 x 749	**B**	**0.092**	**0.018**
2002	c1	600 x 600	**C**	**0.160**	**0.018**
2002	c2a	138 x 138	**D**	**0.190**	**0.018**
2002	c2b	134 x 134	**D**	**0.210**	**0.018**
2002	c3	218 x 218	**D**	**0.224**	**0.018**
2002	d1	738 x 738	B	-0.004	1.000
2002	d2	307 x 307	**B**	**0.096**	**0.018**
2002	e1	959 x 959	B	0.015	1.000
2002	f1	197 x 197	**C**	**0.153**	**0.018**
2002	g1	135 x 135	**C**	**0.154**	**0.018**
2003	j1	1395 x 1395	A	NaN	NaN
2003	k1	1377 x 1377	A	NaN	NaN
2003	l1	438 x 438	A	NaN	NaN
2003	m1	168 x 168	B	0.016	1.000
2003	n1	172 x 172	B	0.023	1.000
2003	o1a	189 x 189	**B**	**0.037**	**0.018**
2003	o1b	115 x 115	**C**	**0.134**	**0.018**

4.4.4. Individual Idiosyncrasies at the Theme Sequence Level

The song level LD analysis results showed a generally higher song similarity among individuals singing the 2002 song type compared to the 2003 song. While in 2002 the average LSI similarity scores with and without phrase repetition were respectively 0.579 (*SD* = 0.158; Figure 4.11A) and 0.755 (*SD* = 0.147; Figure 4.11B), in 2003 the average LSI similarity scores decreased to 0.407 (*SD* = 0.221; with phrase repetitions; Figure 4.11D) and 0.563 (*SD* = 0.211; without phrase repetitions; Figure 4.11E).

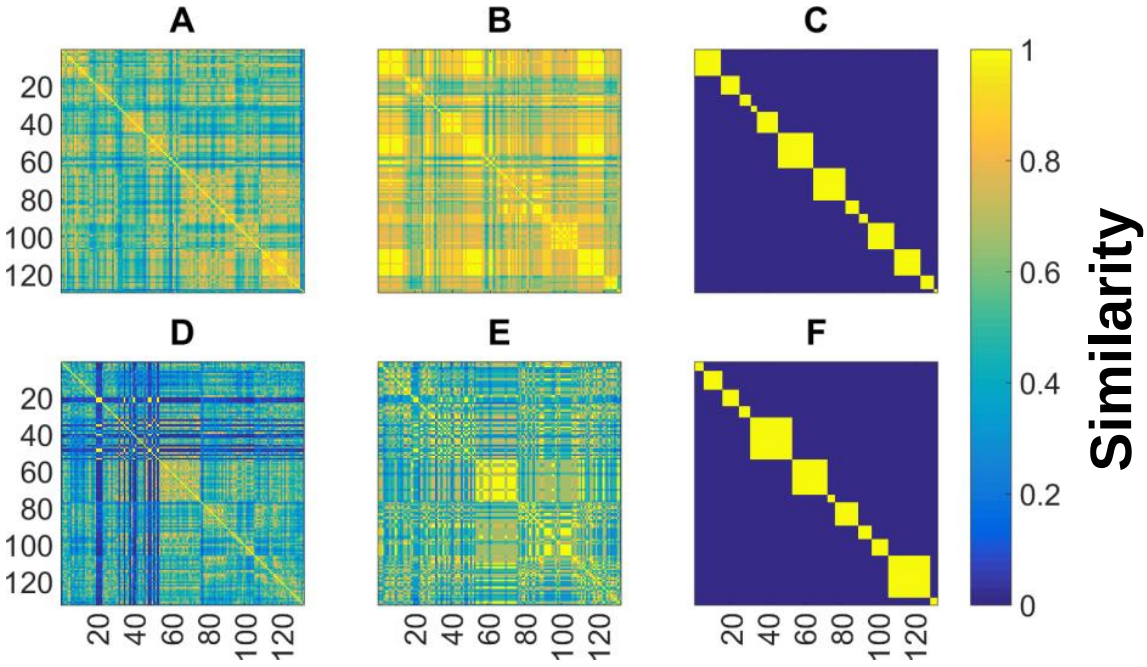

Figure 4.11. Matrices used for the Mantel tests at the song level. The correlation between the 2002 song LSI matrices - with within-theme phrase repetition (A) and without it (B) - and their corresponding IBM matrix (C) were calculated. In the same fashion, Mantel correlations for the 2003 song sequences were calculated using the LSI matrices - with within-theme phrase repetition (D) and without it (E) – and their corresponding IBM matrix (F). Each yellow square in the IBM matrices represents one individual; its size indicates its sample size (i.e. number of song cycles recorded). In a scenario of complete convergence all individuals in the LSI matrix display maximum similarity scores whereas in a scenario of complete individuality the LSI and IBM matrices would be identical.

I performed multiple Mantel tests to quantify the correlations between the 2002-2003 LSI matrices and their corresponding IBM matrices (Figure 4.11, Table 4.4); for each song type I ran the test twice, with and without phrase repetitions. This allowed me to quantify if individual song patterns, when present, were affected by phrase repetition.

Table 4.4. Mantel correlation coefficients and their corresponding p-values for all songs sung in 2002 (light shading) and 2003 (dark shading). Significant correlation coefficients are shown in bold. All the original *p*-values were < 0.001; they have been subsequently adjusted using a Bonferroni correction.

Song type	*Matrix size*	*Within theme repetitions*	*Mantel Correlation r*	*p-value*
2002	129 x 129	Y	**0.276**	**0.004**
2002	129 x 129	N	**0.264**	**0.004**
2003	132 x 132	Y	**0.146**	**0.004**
2003	132 x 132	N	**0.172**	**0.004**

All correlations tested were significant (Table 4.4); the 2002 LSI song matrix displayed a Mantel correlation of 0.276 when within-theme phrase repetitions were included, this correlation slightly decreased to 0.264 without repetitions. The Mantel test on the 2003 LSI song matrix resulted in lower correlation coefficients: 0.146 and 0.172 with and without phrase repetitions respectively. The results of the Mantel tests carried out on the two song types allowed me to reject the null hypothesis that the LSI and IBM matrices were unrelated, which indicated a higher song similarity within rather than between individuals. Within individual song similarity was higher in 2002 than 2003 with $r \sim 0.27$ in 2002 compared to 0.15 in 2003. Phrase repetitions in themes seemed to increase within-individual similarity in 2002 but show the opposite effect in 2003.

4.5. Discussion

In this study I investigated inter-individual song similarity among humpback whales recorded off eastern Australia over two successive breeding seasons that encompassed a song revolution. I found that inter-individual song variation depended on both the level of analysis and on which element was being examined at a given level. Furthermore, although conformity is a fundamental feature of humpback whale songs, significant inter-individual differences did exist in both an evolutionary and revolutionary cultural evolution context. This work had multiple motivations. Population level song conformity among humpback whales is observed worldwide (Cholewiak et al., 2012); however, few studies have focused on investigating inter-

individual variability at different levels of the song hierarchy. Furthermore, non-human cultural phenomena at the scale of the song revolutions observed in eastern Australia have not been described in any other species in which population/colony song conformity is present (Payne, 1985; Trainer, 1989; Noad et al., 2000). Therefore, measuring how individuals respond to such a dramatic change of acoustic repertoire can help us better understand this cultural phenomenon as well as providing insights into potential mechanisms of song learning. Finally, a growing body of research across multiple taxa such as birds (Robisson et al., 1993; Charrier et al., 2001; Jouventin and Aubin, 2002; Berg et al., 2011), terrestrial mammals (Vannoni and McElligott, 2008; Arnold and Wilkinson, 2011; Jansen et al., 2012; Salmi et al., 2014), and marine mammals (Ford, 1991; Rendell and Whitehead, 2003, 2005; Janik et al., 2006; Sayigh et al., 2007), has unveiled how high inter-individual call variability can be linked to the advertisement of identity, fitness or reproductive status to conspecifics, which is relevant where we do not understand how such processes work in the humpback song display.

4.5.1. Sub-phrase Inter-individual Variability

My analysis focused first at the most basic hierarchical level, looking at how units were combined to form sub-phrases. Inter-individual variability among the sub-phrase types analysed in this study was not homogenously distributed. Based on my pool of singers and their median sub-phrase strings (Figure 4.3), sub-phrases formed by the combination of 2-4 units were generally sung very consistently both between and within individuals in both the evolutionary song of 2002 and the revolutionary song of 2003. Good examples of this type of high conformity across individuals were sub-phrase types e1 (3 units) and d1 (2 units) for the 2002 song type and j1 (2 units), k1 (2 units) and l1 (2 units) for 2003 song type. Predictably, themes that comprised more than four or five units (including also repeats of the same unit type) were generally more variable. Based on my results, two main sources of sub-phrase variability were highlighted.

The first and most common type of variability was found in sub-phrases that included varying numbers of repeats of the same unit type. For example the number of

'grunts' (GR) repeated in sub-phrase types c1 and m1 varied within each individual with no apparent individual trend (Figures A4.3 & A4.4 for individual GR repeat distributions). In general, the repetition of the same sound element might have different functions. For example, it can be used as a proxy to convey fitness information in rock hyraxes (*Procavia capensis*) where larger individuals are able to produce more numerous and longer 'chuck' calls bouts (maximum chucks repeats was 51) compared to smaller individuals (mean number of chuck repeats in the study sample was 12.8±10; Koren and Geffen, 2009). Moreover, repeating the same sound element can function also as a compensation mechanism to maintain communication efficiency in unfavourable conditions (Lengagne et al., 1999; Miller et al., 2000). In humpback whales, variation in phrase repetition has also been linked to both behavioural context (Smith, 2009) and to exposure to anthropogenic noise (low-frequency active sonar; Miller et al., 2000). However, within-phrase unit repetition has only been taken into account within the study of sound production, associating the repetition to particular states of the sound production organs (Adam et al., 2013). My results suggested that the repetition of the same unit might be variable both within and between individuals (Figure A4.3 & A4.4); however, examples where specific unit repetition resulted in distinctive individual patterns (i.e. idiosyncrasies) were also present.

The second source of inter-individual variability in sub-phrases was combinatorial, with different individuals arranging the pool of units of the same sub-phrase in different ways. A clear example is seen in the median sub-phrases c2a and c2b (Figure 4.4 & Table A4.1). This type of variability was also found in humpback whale songs off the Brazilian coast; singers sequenced the same phrase type with different proportions of 'simple' and 'complex' units (Arraut and Vielliard, 2004). The ability to form different combinations of sounds has been described in several species. In several songbird species (*Luscinia megarhynchos*, *Sturnidae* sp. and *Lonchura striata domestica* just to cite three examples) meaningless sounds can be combined in sequences that convey the same 'message', forming a 'phonological syntax' (Kroodsma and Momose, 1991; Marler, 1998; Berwick et al., 2011; Collier et al., 2014). Less often, meaningful sounds combined in different ways might convey crucially different information to conspecifics (Ouattara et al., 2009a; Ouattara et al., 2009b; Jansen et al., 2012; Suzuki et al., 2016), therefore constituting a 'lexical syntax' (Marler, 1998;

Collier et al., 2014). For example, male putty-nosed monkeys (*Cercopithecus nictitans*) produce two types of alarm calls: 'pyows' are used in the presence of a leopard (*Panthera pardus*) while 'hacks' are produced as an alarm for crowned eagles (*Stephanoaetus coronatus*). When the two calls are sequenced together they form a third structure, P-H sequences, which elicit group displacement, hence changing the original meaning of the two calls (Arnold and Zuberbühler, 2006). It is difficult to conclusively place humpback whale songs, a sexually selected trait, on the continuum formed by phonological and lexical syntax. However, considering the dual nature of the sub-phrases found in both songs (presenting low or high inter-individual variability) and the combinatorial variability shown in some sub-phrases, it might be hypothesised that different portions (intended as sub-phrase types) of the song as well as alternative unit combinations in specific sub-phrases might have different purposes within the general mating function of songs. Therefore, humpback whale songs could be interpreted within a multiple-messages framework, in which different parts of the signal might convey more than one type of information such as species recognition (or potentially population, in the case of humpback whales) and signaller quality (Hebets and Papaj, 2005). A recent study of the eastern Australian population using different song types and partially different methodologies reached the same theoretical conclusion (Murray et al., 2018) to the one hypothesised here.

4.5.2. Song Level Inter-individual Variability

The song level analysis showed a clear structural contrast between the theme sequences that formed the evolutionary song of 2002 and those of the revolutionary song of 2003. This difference was apparent in multiple ways. The total theme repertoire of the 2002 song type was more than double the 2003 song type (16 themes vs. 7 themes, Table 4.2),although it must be noted that seven 2002 themes were sung in less than 15% of the song cycles. Moreover, both the number of unique themes for all songs (Figure 4.5) and median theme sequences (Figure 4.8) highlighted a structural distinction between the two song types. Individuals from 2002 used on average more themes per song than the 2003 singers. Inter-individual song variability also differed between the two song types. In 2002, there was a general degree of similarity among individuals, with few exceptions like whale ID 14 and ID27 (Figures 4.6A, 4.8 & 4.9B).

By contrast, in 2003, two main clusters arose from the song similarity analysis at a higher dissimilarity level (dissimilarity level = 4; Figure 4.7A) compared to the highest clusters observed in 2002 songs (dissimilarity level = 2.5; Figure 4.6A). Thus there were two quite dissimilar variations on the basic song in 2003, a shorter and a longer one, the latter including themes M1, N1, O1a and O1b. This result was also consistent with median theme sequences (Figures 4.8, 4.9C &D) despite some individuals that presented a short median theme sequence also sporadically sang the longer song version.

The disparity in the theme content of the two songs and the different levels of inter-individual variability in my sample could potentially be attributed to the different nature of these two song types. In between revolutions, songs undergo cultural evolution with the addition of new units and the lengthening of units and phrases (Payne et al., 1983; Payne and Payne, 1985; Cerchio et al., 2001). The relatively rich repertoire of units/sub-phrases/themes and the relatively low inter-individual variability displayed by singers in 2002 compared to 2003 could have resulted from this cultural evolution of the song type. The origin of the 2002 song type is uncertain but can be traced back to at least 2000 (Garland et al., 2011). However, given no other song revolutions were documented between 1998 and 2003 (Rekdahl, 2012), the 2002 song may be a result of the song introduced in eastern Australia with the 1998 song revolution (Noad et al., 2000). The population therefore had had time to reach high levels of overall song conformity through convergent learning. The higher inter-individual variability in theme sequencing (and presence) displayed in 2003 could by the same reasoning therefore be due to the recent acquisition (during the breeding season and/or migration prior to recording) of this song type by the eastern Australian population. Therefore, it could be hypothesised that theme level variation between individuals in my 2003 sample might reflect variable learning abilities – more specifically, the speed at which they could radically change their song repertoire. This hypothesis could be tested by an in-depth analysis of the inter-individual variability of a comparable number of singers before and after other song revolution events.

4.5.3. Individual Idiosyncrasies

The relationship between inter- and intra-individual variability both at the sub-phrase and song level highlighted the presence of individual patterns (or idiosyncrasies) among the singers in my sample. While for some sub-phrase types intra- and inter-individual variability were completely absent (Figure 4.10A), for others the variability within and between individuals was equivalent, as shown by low Mantel correlation scores (Figure 4.10B, Table 4.3). In the case of sub-phrase types d2, f1, g1 and o1b, one singer consistently sang a modified, individually unique version of each sub-phrase (Figure 4.10C). In the fourth and final case, comprising sub-phrase types c2a, c2b and c3 multiple individuals sang individually unique versions of the sub-phrase (Figure 4.10D, Table 4.3).

At the song level, the 2002 song cycles showed a higher presence of individual patterns regardless of whether phrase repetitions within themes were considered, compared to 2003 (Table 4.4) despite overall song similarity among individuals being higher in 2002 than 2003 (2002 mean LSI coefficient 0.755, *SD* = 0.147; 2003 mean LSI coefficient 0.563, *SD* = 0.211; Figures 4.11B & E). These results suggest that fine scale changes both at the sub-phrase and song level are present and may help a singer/male 'stand out' acoustically from their conspecifics.

Within the dataset, an example of a singer that managed to stand out by showing various examples of individual idiosyncrasies was whale ID14. Excluding the use of theme C1d (only used by singer ID27 in the 2003 breeding season), ID14 theme sequences displayed high similarity with the 2002 song type displayed by the majority of singers; however, when sub-phrases were taken into consideration ID14 produced consistent unit sequences that were different to those produced by the rest of the singers in my sample. It was the only individual to sing two additional sub-phrases (i1 & h1) that encompassed the production of unit types unheard in other sub-phrases (theme H1, Figure A4.1 & Table A4.1), which is noteworthy considering the amount of general conformity shown in the 2002 song type. Moreover, it sung sub-phrases c1, c2a and c3 with consistent unit changes compared to all the other individuals. Generally, in sub-phrase c1 it deleted the initial 'ascending-moan' (AM) (Figure A4.1, Table A4.1),

increased the repetition of ‘grunts’ (GR) (Table A4.1 & Figure A4.3), and added occasionally ‘whoops’ (WO) to the sub-phrase. Similarly, in sub-phrase c2a and c3 it omitted the initial ‘ascending-moan’ (AM) (Figure A4.1) and displayed a distinctive combination of ‘trumpets’ (TR) and ‘n-shaped shrieks’ (NSH). ID14 also showed a high similarity in sub-phrase c1 with whale ID27 (Table A4.1, Figure A4.3) which was recorded a year later, in 2003. Singer ID14 is an interesting example because following definitions in some literature it would potentially be considered an ‘aberrant’ singer (Frumhoff, 1983); however, at closer examination this individual generally conformed to the 2002 song type while concurrently displaying multiple unique features, both at the sub-phrase and song level, making its song simultaneously distinct from all the other individuals in the sample and fitting to the general structure of the 2002 song. This apparent paradox of distinctiveness versus conformity echoes a similar example observed in two suboscine birds (*Hypocnemis peruviana* and *H. subflava*). These two closely related species of antbird produce convergent songs in dense, diverse and noisy tropical habitats. Despite the high inter-specific song conformity, females are able to discriminate between species and individuals using extremely subtle cues that males provide in their songs (Seddon and Tobias, 2010). Although it would be unwise to infer that this paradox applies to humpback whales based only on one individual’s songs, individual idiosyncrasies such as those displayed by ID14 should be investigated more thoroughly in future studies.

There were no examples of individual idiosyncrasies at the sub-phrase level in the 2003 data, with the exception of sub-phrase o1b, in which whale ID17 sang more repetitions of ‘bird-whistles’ (BW) compared to the rest of the other whales (Table A4.2). However, it has to be noted that ‘bird-whistles’ were high frequency units (see Figure A4.2 for spectrogram), usually quite low in amplitude and therefore sometimes challenging to detect and classify. At the song level, individuals ID6, 7, 9 and 10 consistently sang just three themes while others (e.g., ID2 & 4) sang more complex theme sequences featuring six to seven themes (Figure 4.7A, 4.8, 4.9C &D).

The wide scale disparity in theme production by individuals in 2003 as well as the fine scale, individually distinct, sub-phrase modifications seen in the 2002 song type confirmed that although conformity at all hierarchical levels is a consistent feature of

humpback whale songs, individually distinctive patterns of production are widespread. The current results support the suggestion of Arraut and Vielliard (2004) that individuals differ in their ability to learn and compose songs. In general, factors such as age, personality traits, developmental stress and reproductive state are known to affect learning abilities across species (Thornton and Lukas, 2012; Mesoudi et al., 2016), but unfortunately individual life histories are unknown for my pool of singers. Some evidence suggests that different portions of the songs might however play different functions during the mating display (Hebets and Papaj, 2005; Smith, 2009; Murray et al., 2018). It would be consistent with findings from other species (Hasselquist et al., 1996; Neubauer, 1999; Boogert et al., 2011) if, within the inherent cognitive constraints of song production (Cerchio et al., 2001), a wider (or novel) repertoire of units and/or themes were to be positively selected for by females (Noad et al., 2000; Smith et al., 2008). Considering the continuously evolving nature of humpback whale songs and the potential key role of novelty in song selection by females, a singer on the leading edge of evolutionary song change (i.e. learning quicker than the others and therefore demonstrating better quality mate characteristics) may benefit from a higher reproductive success compared to 'slower' learners. This is part of the novelty-threshold hypothesis formulated by Noad (2002), and the individual patterns observed in this study fit well into this theoretical framework. An example of what Noad (2002) defined as 'leaders' - individuals at the 'vanguard of song change' – could be the singer ID14, which displayed a higher number of themes with multiple sub-phrase individual idiosyncrasies within a highly conformed evolutionary song. Conversely, a 'follower' – an individual that learns more slowly – might be identified in the 2002 dataset as singer ID27. This individual sang the 2002 song type in 2003, after the new revolutionary song type had been introduced and apparently adopted by most of the population, perhaps displaying a low learning ability. Within the 2003 songs, differences between apparent 'leaders' and 'followers' are more extreme than in 2002. Singers such as ID2 and ID4 showed a larger theme repertoire size, demonstrating their acquisition of the entire new song repertoire more quickly than singers like ID6, 7, 9 and 10, which produced only a partial, simplified, version of the entire acoustic display. On the other hand, individuals that depart from the general conformity of their respective song types have been historically referred to as 'aberrant' (Frumhoff, 1983) and therefore one of the pressing

questions that future studies will have to address is the discernment between what is considered ‘aberrant’ and what constitutes the ‘vanguard of song change’ in humpback whale populations that experience periodical song revolutions.

In conclusion, in this study I quantified intra- and inter-individual song variability, identifying fine-scale individual patterns at level of both the sub-phrase and the song theme sequence, while still confirming the general population-level song conformity observed in all humpback whale populations. The results presented here reveal a complex scenario in which inter-individual variability is not found homogeneously across the song structure. While some sub-phrase types displayed high variability between individuals, others showed a complete lack of it, and variation both within and between individuals indicated potentially different sub-phrase functions. Distinct individual patterns were found in both sub-phrases and songs, with differences between the evolutionary and revolutionary song type analysed here. These results suggest that within the constraints of a highly conformist vocal system, male humpback whales are able to produce individually distinctive patterns that might be functional in advertising their quality as potential mating partners. Future studies will need to confirm these results by conducting a similar analysis on a larger and diverse song sample size incorporating multiple revolutions and longer periods of evolutionary change. Moreover, in order to understand what constitutes a whale being at the forefront of song evolution, as opposed to being simply aberrant, it will be critical to look at individual life histories, correlating song characteristics and idiosyncrasies with external factors such as age, paternity success, and female preferences.

Chapter 5

General Discussion

5.1. Novel Contributions

In this thesis I investigated the cultural evolution of humpback whale songs using theoretical and empirical methods. Two general approaches characterised the inception and development of this thesis: First, the interdisciplinary approach used to develop the theoretical models and second the bottom-up approach used to seek insights about individual learning by reverse-engineering from collective behavioural characteristics of humpback whales. The inception of the thesis project was guided by the idea that cross fertilisation between apparently distant academic fields can be extremely fruitful in providing new insightful perspectives on a particular topic. Here I used an interdisciplinary approach to adapt an agent-based model framework conceived to study the emergence of musical culture in humans (Miranda, 2003; Miranda et al., 2003; Miranda et al., 2010) to investigate the ecology and acoustic behaviour of humpback whales. Agent-based modelling has been already used as a tool to study the acoustic behaviour of other marine mammal species such as killer whales and sperm whales (Cantor et al., 2015; Filatova and Miller, 2015). However, none of these past studies dealt with an acoustic displays as complex as humpback whales' songs; furthermore, while in these previous studies (Cantor et al., 2015; Filatova and Miller, 2015) the modelling effort was predominantly focused on the acoustic behaviour, here the model design took into consideration the spatial movement of individuals as well as their acoustic behaviour and cognitive abilities. The spatially explicit modelling component presented in this thesis was inspired by studies on animal collective moment (Couzin et al., 2002) and is demonstrated to be of fundamental importance in obtaining some of the results presented here. The agent-based model design developed during this thesis constitutes a novel contribution to the investigation of animal cultural evolution because of its comprehensive modelling approach, which was inclusive of aspects such as the movement and acoustic behaviours of individuals, as well as the potential physical and cognitive biases governing their interactions.

The second general characteristic common to all the chapters presented here is the use of a bottom-up approach in which individual behaviours were the focus of the analysis; in other words, by investigating the behaviour of individuals, either virtual agents or actual humpback singers, I hoped to uncover some of the mechanisms underlying the cultural evolution of humpback whale song. Agent-based models are by design bottom-up simulations of a system in which the individual interactions among agents (and their environment) might result in the emergence of population-level phenomena. Here, I exploited this modelling technique to investigate the learning mechanisms involved in the striking collective behaviours observed in the humpback whale song system. Furthermore, my focus on individual behavioural features was not only limited to theoretical models, but also to understand how actual songs varied between individuals and what inferences could be made on humpback whale song learning based on inter- and intra- individual variability. Previously, few studies had investigated song variability across individuals by comparing the variation of acoustic features of some of the sounds produced (Guinee et al., 1983; Frankel, 1996; Macknight et al., 2001; Arraut and Vielliard, 2004). However, here I shifted my attention from measuring the acoustic properties of sounds to comparing, both within and between individuals, the way in which they are sequenced together in songs. The level of hierarchical detail reached in this analysis as well as some of the new analytical methods applied to the investigation of individual distinctiveness in songs provide new insights into the potential function of humpback whale songs and the way evolution and revolution could influence song learning and advertisement.

5.2. Summary of Findings

In chapter 2, a spatially explicit agent-based model was developed to understand the individual learning mechanisms that drive both song conformity and evolution in humpback whale songs. The mechanisms that drive the dual modes of song change, evolution and revolution, are not currently understood, and logistical difficulties in tracking individual whales, and their acoustic behaviour, over long migratory routes are enormous, so modelling is a pragmatic research approach. The model tested a range of cognitive biases that may be responsible for driving changes in the song, such as a bias towards novel songs, production errors, and the coupling of novelty bias and production

errors. None of the models showed population song revolutions, however, they did show that shared feeding grounds where agents from separated populations mixed facilitated song cultural transmission. Furthermore, geographically isolated breeding grounds promoted song divergence while production errors allowed song to gradually change over time. The results presented in this chapter suggested that while other cognitive biases could be at play in the emergence of song revolutions, a simple instinct to copy any song heard according to how loudly it is heard, coupled with production errors when singing, can lead to population level conformity to distinct song variations matching the evolutionary mode of song change.

In chapter 3 I built upon the results of the previous chapter and focused solely on song revolutions. The models' shortcomings highlighted in chapter 2 were addressed by introducing new movement scenarios and a new cognitive bias in order to produce hypotheses regarding the individual behavioural rules at the origin of the song revolution events recorded in eastern Australia. Two populations of agents were designed to simulate the western and eastern Australian populations and spatial overlap and the individual movements between these two agent populations were manipulated under three distinct movement scenarios. Song revolutions occurred in the first movement scenario, in which whales mixed on shared feeding grounds, only when large proportions of both populations overlapped spatially. In the second and third movement scenarios, involving individual whales switching populations, models that featured a learning bias modulated by song memory showed consistent song revolutions with (1) high conservatism towards pre-existing memory, (2) high agent density in the feeding grounds and (3) low singing probability during the feeding season. These results suggested that these three factors could all be crucial aspects of song learning leading to the revolutionary changes observed in the South Pacific.

In chapter 4, I continued to investigate the role of humpback whale individuals in song learning and evolution by measuring individual level variation in the degree to which their songs, recorded off eastern Australia, conformed to one another. Furthermore, I investigated the presence of individually distinctive patterns at different song hierarchical levels. Individually distinctive acoustic signals in animal vocal communication are taxonomically widespread and, until now, their investigation in

marine mammal species has focused mainly on odontocetes such as bottlenose dolphins, killer and sperm whales. While humpback whale songs have been studied extensively for more than forty years, little effort has been dedicated to quantify fine-scale conformity, and inter-individual variability has been described in just a few cases, with contradictory results. In order to fill this knowledge gap, I quantified intra- and inter-individual variability at different levels in the song hierarchy (sub-phrases and songs) of 25 distinct singers. I used two song types: the song sung in eastern Australia in 2002, and the revolutionary song introduced into the same population the following year. The results suggested that inter-individual song similarity was not homogeneous, but instead that the different song hierarchical levels presented variable degrees of inter-individual similarity. As an example, some sub-phrase types were sung very consistently by all singers while others displayed high inter-individual variability. Furthermore, distinct individual patterns were found in both sub-phrases and songs, with differences between the evolutionary and revolutionary song type analysed here. These results suggested that within the constraints of a highly conformist vocal system, male humpback whales were able to produce individually distinctive patterns that might be functional in advertising their quality as potential mating partners, and support existing hypotheses about understanding humpback song as containing 'multiple messages' (Murray et al., 2018).

5.3. Main Features of Humpback Whale Songs

Among the many complexities and paradoxes that humpback whale songs display, there are three fundamental features that distinguish humpback whale songs from most of other animal acoustic displays: population level song conformity, gradual song evolution and occasional rapid song revolution.

5.3.1. Song Conformity

The main characteristic of the humpback whale song system is the high degree of vocal conformity displayed by males from the same population (i.e. individuals in acoustic contact). Song conformity has been recorded within populations all over the world (Payne and Payne, 1985; Cerchio et al., 2001; Cholewiak et al., 2012) and it definitely represents one of the main drivers of humpback whale song learning. Song conformity is maintained even if songs are in constant evolution as individuals seem to

always sing the most updated version of the vocal display (Frumhoff, 1983; Payne et al., 1983; Payne and Payne, 1985).

The results of the agent-based models developed in chapter 2 showed how, with the model that made the least assumptions on the cognitive abilities of humpback whales, within population song conformity and between population song divergence emerged as a function of sound transmission loss and the spatial arrangements of breeding and feeding grounds. Smaller feeding and breeding grounds drove agents closer together increasing their spatial density resulting in higher levels of song conformity. Although the magnitude at which song conformity occurs in humpback whale populations involves entire populations of individuals, these results are in line with similar theoretical studies that looked at the origin of birdsong dialects (Goodfellow and Slater, 1986; Williams and Slater, 1990). Furthermore, high population density has been suggested to influence song sharing, and therefore song convergence (Lachlan and Slater, 2003).

If songs are learned from individuals in the learner's geographical vicinity during his sensitive learning period (Catchpole and Slater, 2008a), limited dispersal and cultural drift can result in the emergence of song dialects (Toews, 2017), or song types in the case of humpback whales, which are then used and maintained to convey information about group/population membership to females and to isolate intruders (Kroodsma, 2004; Lachlan et al., 2004; Wright and Dahlin, 2018). The different levels of inter-individual variability encountered in chapter 4, with some sub-phrase types presenting no variability and others displaying high individual distinctiveness, could be part of a multi-message display in which the high level of conformity of certain sub-phrase types convey to females the population membership of the singers (Hebets and Papaj, 2005; Murray et al., 2018).

However, acoustic conformity could be driven also by cognitive biases. As an example, male village indigobirds (*Vidua chalybeate*) show within-colony song conformity, and young individuals (as well as young Indigo Buntings, *Passerina cyanea*) seem to change their songs based on a model bias and converge towards songs sung by older more successful individuals in the colony in order to increase their mating success (Payne, 1982, 1985; Hoppitt and Laland, 2013). The inter-individual song

variability showed in chapter 4 could be interpreted in terms of a similar type of learning process. Assuming females prefer more complex songs, the variability in theme repertoire, especially evident after the song revolution of 2003 occurred, could be originating from older more successful individuals singing more complex and comprehensive versions of the vocal display compared to young unexperienced individuals producing relatively incomplete, more aberrant, renditions of the song (Tyack, 1981; Frumhoff, 1983; Payne et al., 1983). On the other hand, the opposite process could be inferred as well if females choose males based on their song novelty, or the speed at which males can incorporate novelties in their songs (Cerchio et al., 2001; Noad, 2002); experiments of induced diffusion of behavioural traits suggest that, within a conformist system, young individuals showed higher flexibility and speed in switching between foraging traditions compared to slower older conspecifics (Aplin et al., 2017). Currently, it is difficult to confidently ascribe humpback whale song learning to either of these cognitive biases; however, future studies that will concurrently track song changes and age of individual singers (Polanowski et al., 2014) will be provide valuable data to reduce this uncertainty.

5.3.2. Song Evolution

The second general feature encountered in humpback whale populations all over the globe is the gradual change that characterises the songs. The song elements such as units and themes are constantly rearranged, split, omitted or substituted in a progressive unidirectional change defined as song evolution (Winn and Winn, 1978; Payne et al., 1983; Payne and Payne, 1985; Cato, 1991), which occur both within and between breeding seasons (Guinee et al., 1983). While it is clear that song changes are culturally transmitted between individuals, the mechanisms behind song evolution are still debated. Some authors suggest that song novelty or complexity could be favoured by female preference (Tyack, 1981; Payne et al., 1983; Cerchio et al., 2001), pushing males to constantly modify their songs in order to either stand out from the acoustic background and/or avoid female habituation, as seen in some songbirds (Searcy et al., 1994). Other authors suggest that production errors, drift and potentially improvisation could also be factors at play in the evolution of songs (Payne and Payne, 1985).

Chapter 2's results suggested that, in a modelling scenario in which learning was influenced only by sound transmission loss, a low production error probability (mainly theme insertions) could prevent the collective song system from reaching a complete and unrealistic conformity, promote song divergence when populations were geographically isolated, and finally allow songs to constantly change over time. Given that I modelled songs at the theme level, caution should be taken in interpreting these results at the phrase and unit level. Nonetheless, it is interesting that a low production error probability could still produce theme sequences comparable, in their variability, to the ones recorded in the wild.

The analysis conducted in chapter 4 highlighted how individual variability is present at different levels of the song hierarchical structure. At the sub-phrase level, individuals showed variability even between renditions of the same sub-phrase types, especially when it came down to repetition bouts of the same unit types. We are a long way from understanding whether this within-individual unit variability is conscious or functional to a specific behavioural context (Lengagne et al., 1999; Miller et al., 2000; Koren and Geffen, 2009); the most parsimonious explanation would suggest this type of intra-individual variability, which could be interpreted as production errors, could drive, at least partially, the continuous evolution of songs by promoting song drift (Payne and Payne, 1985).

On the other hand, the results of chapter 4 also showed also how some song elements could display complete consistency within individuals and high distinctiveness between individuals. This kind of inter-individual distinctiveness could be explained by a preference of females for novel songs (or elements of it) that drives males to produce distinctive patterns while maintaining a general conformity to the population's specific song (Cerchio et al., 2001; Noad, 2002). Most likely, the novelty preference of females has an optimum beyond which unstructured and aberrant song are not positively selected (Cerchio et al., 2001). Therefore, the speed at which males are able to produce and/or learn novelties could be the trait selected by females as a potential measure of cognitive fitness. Following this reasoning, males at the vanguard of the song evolution ('leaders') would be expected to have more mating success than males than need more time and acoustic exposure to acquire novel songs and/or novel song elements

('followers'; Noad, 2002). The inter-individual variability at both the sub-phrase and song level and the example of individual distinctiveness observed in chapter 4 seemed to fit well with this theoretical framework.

Furthermore, based on the modelling results on song revolutions (chapter 3) it could be hypothesised that spatial dynamics could also be involved in the speed of acquisition of novel song variants. In the models of song revolutions, individuals did not acquire the revolutionary song type all at the same time due to the spatial stochasticity inherent in the modelling approach. However, what is driven by stochasticity in the model could be partially influenced by fitness, physical condition, weather, other species, and a whole myriad of other factors in the wild. In other words, a hypothetical male that migrates faster to a feeding ground will have a longer time of exposure in which to potentially acquire song novelties (or, like in the case of revolutions, an entirely new song type) and therefore it will be able to produce the most updated and complete version of the song once he returns to his breeding ground, resulting in a higher mating success. Naturally, this hypothesis is highly speculative but could inform future empirical research on individual males, their song changes and their mating success that will help us understand these aspects of song evolution.

5.3.3. Song Revolution

Song revolutions consist of the complete and rapid replacement of a population's song type by the introduction of a novel song from an adjacent population, presumed to occur either through acoustic contact in the feeding grounds or through movement of individuals within a breeding season (Noad et al., 2000). The only area of the globe where revolutions have been documented is the South Pacific (Garland et al., 2011), and this is probably related to the geographical isolation of breeding grounds and the spatial overlap between populations in the feeding grounds (Olavarría et al., 2007; Schmitt et al., 2014; Rosenbaum et al., 2017). In all of the five song revolutions recorded so far in eastern Australia, the revolutionary song always came from the western Australian population (Noad et al., 2000; Garland et al., 2011; Rekdahl, 2012).

The mechanisms that trigger song revolutions are still poorly understood. Asking why, in a highly conformist song system, an entire population of males quickly

abandons their previous song in order to acquire a completely new song type presents a paradox. To explain this process, it is hypothesised that males switch song types to acquire a more novel song, assuming novelty is positively selected by females (Noad et al., 2000). The results of the models run with a novelty bias (chapter 3) suggested that novelty alone, or at least my interpretation of it, was not sufficient to trigger a complete song replacement. Conversely, the models in which agents were equipped with a memory to store songs produced consistent song revolutions. The difference between the two learning biases (novelty and memory) came down to the directionality of learning. Assuming a hypothetical immigrant agent joining a population of residents in their feeding grounds, when I used the novelty bias the learning process was symmetrical, in the sense that both the immigrant and the residents equally recognised novelty in each other songs, resulting in a hybrid song for all agents, in which all songs were potentially possible and none dominated. In contrast, when I equipped agents with a song memory and a specific combination of parameters were in place (establishing high agent density, high memory conformism, and low singing probability on feeding grounds) the learning dynamic between the immigrant and the residents became asymmetrical, resulting in song revolutions being the most frequent model result.

The model results produced using the memory-modulated learning bias provided new insights that can be interpreted as part of the current theories of song learning and evolution in humpback whales. This learning bias drove the agents to increase their learning effort if exposed to songs different from the ones learnt in their own population. I argue that this is an alternative, and potentially more realistic, implementation of how whales would react to novel songs. This formulation of novelty based on song memory and the subsequent song revolutions it produced seem to confirm the theory that indicates novelty as a primary driver of song evolution and revolution (Noad et al., 2000; Cerchio et al., 2001). In conclusion, the revolution models' results suggest that currently unexplored aspects such as song memory and the singer's sense of how well its song might fit the acoustic song-scape that surrounds him might in fact have a role in the occurrence of song revolutions in the wild.

5.4. Model Critique

When trying to simulate a natural system, the modelling design constantly has to face a compromise between complexity and abstraction. An over-complicated model, which tries to capture the full complexity of the natural system it intends to investigate, will likely be over-parametrised and computationally infeasible; furthermore, due to the large number of parameters involved, its results would be difficult to interpret. On the other hand, an over-abstracted model would not be tailored enough to the characteristics of the target species, therefore, its results would be too broad to produce useful and testable species-specific hypotheses. Striking a balance between these two extremes has been one of the biggest challenges of the modelling efforts I carried out in this thesis. While there were areas of the model in which the balance between complexity and abstraction was optimally found, in others it was more difficult.

The time and spatial scales in which the agents of the models designed here moved were not fully realistic and representative of humpback whale ecology. The agents' migratory cycle comprised 12000 iterations, the ratio between the number of iterations was set in order to mimic the different seasons encountered during a year by humpback whales. If a year were to be divided by 12000, each model iteration would then represent approximately a 45 min time window. It is unlikely that the amount of song production, learning and movement simulated in the models presented here would occur in the wild in such a short time frame. Furthermore, the distance between the feeding and breeding grounds was set to fit in the proportion of iterations allocated for each season (i.e. to allow the agents to cover the distance in the amount of iterations available), considering, at the same time, also the maximum speed (1 spatial unit) at which agents could travel on the Cartesian plane during a single iteration. Another spatial aspect that was difficult to set in accordance with the overall distances covered by the agents while migrating was the design of the zones of repulsion and attraction (ZOR and ZOA). In chapter 2, ZOR and ZOA radiuses were set based on both a parameter space analysis and estimates found in the literature regarding song transmission loss in the field (Winn and Winn, 1978; Cato, 1991; Noad et al., 2004; Dunlop et al., 2007). Based on previous studies, I assumed here that each encounter between singers closer than 100 m would produce inhibition of the singing activity

(Tyack, 1981; Darling and Bérubé, 2001; Darling et al., 2012a; Cholewiak et al., 2018) and that song could be perceived up to 10 km, triggering an attraction towards the singer (Darling and Bérubé, 2001; Darling et al., 2012a; Dunlop and Noad, 2016). I could not directly transpose these distances into the model's Cartesian plane, therefore, I maintained their ratio and applied it into the abstract Cartesian units. The time and spatial scales of the models presented here could have been calibrated more realistically, however, by generally retaining the ratios that characterise these scales in wild humpback whale populations, the hypotheses produced through this modelling framework should still be valid.

The implementation of a song novelty algorithm within the agent-based model architecture was another challenging process to finalise. Song novelty is thought to be one of the main drivers of song evolution and revolution, being potentially selected by females (Noad et al., 2000; Cerchio et al., 2001; Garland et al., 2011); it was therefore necessary to design a novelty algorithm based on this assumption, and to test its potential influence on the agent song evolution. The novelty bias developed in chapter 2, which was inspired by Todd and Werner (1999) investigation on the influence of female choice in the evolution of music, was based on the idea of song expectation. In other words, the more a song sequence is unexpected, based on the listener's own song, the higher its novelty value will be. The novelty value calculated in chapter 2, α, was then used to promote the learning of the unexpected/novel song within the agent learning algorithm.

The implementation of the novelty bias in model experiments of chapters 2 and 3 did not produce any song replacement comparable to that observed during song revolutions. Although in chapter 2 the novelty bias learning algorithm prevented the fixation of the agents' song representation matrices (SR) seen using the distance-only learning algorithm, it also drove all agents SRs towards low transition probabilities, thus increasing unrealistically the variability of an individual song output. Once this point was reached, the experiment song system was always driven towards a static equilibrium, in which transition probabilities remained low and therefore the novelty value of any song produced became equivalent. A similar outcome was hypothesized by Todd and Werner (1999) as a result of implementing only positive novelty scores, and

not negative ones. I tested the learning algorithm also in chapter 3, using different movement scenarios in which a single immigrant agent was introduced into a resident population. Even though novelty performed better than the learning bias based solely on sound transmission loss, it still did not trigger a total population song replacement characteristic of a song revolution. The decreased ability of agents to detect novelty due essentially to the randomization of songs (i.e. low transition probabilities) is an artifact of this novelty implementation and, therefore, other modelling approaches should be tested. Nonetheless, these novelty results could provide a more general perspective relative to the psychology of novelty: in these novelty models the agents demonstrate that in a random environment scenario novelty ceases to exist, as everything becomes expected.

However, it can also be argued that the learning bias based on song memory developed in chapter 3, provides an alternative implementation of a novelty bias. In the chapter 3 experiments in which the memory based learning algorithm was tested, if an agent that was equipped with a song memory was exposed to an unfamiliar song (i.e. it stored the unfamiliar song in its memory), it would increase its willingness to learn and, if exposed again to the unfamiliar song, eventually acquire it in its repertoire. This mechanism could be compared to a perception bias, in which females (and other male singers) would direct their attention, and potentially their learning efforts, towards songs (or elements of songs) that stand out from the song type sung by the majority of individuals (Cerchio et al., 2001; Noad, 2002). The results presented in chapter 3 suggest that a novelty bias formulated in this way (increased learning due to exposure to an unfamiliar song), in combination with other spatial and ecological factors could be important aspects at the origin of the occurrence of song revolutions.

5.5. Future work

The model architecture presented in this thesis was developed over the course of four years, and as any intellectual endeavour it could be endlessly improved, which is, in fact, one of the inherent characteristics of science. The implementation of female agents and individual fitness into the model architecture would definitely provide a new evolutionary perspective. On the other hand, modifications of the song production

algorithm that could help simulate the whole range of complexity of humpback whale songs would increase the realism of the results.

5.5.1. The Role of Females

One of the main improvements that could be implemented in the current model architecture would be the creation of female agents. In the current model formulation all agents are singers, thus representing only male humpback whales. This helped simplify, especially in the beginning, the building and testing of the model. If rules pertaining to the behaviour of females were to be added from the beginning, a challenging layer of complexity would have been added to model testing and parameter space exploration. However, I never lost sight of the fact that humpback whale songs are a sexually selected trait, and that females likely play a fundamental role in the cultural evolution of songs; all of the learning biases developed here have always had the assumption that behind the singers' cognitive choices there were always female preferences that selected for them in the first place. Now that this model and the behavioural rules that constitute it have been thoroughly tested in this thesis, there is a solid modelling base on which the introduction of female agents could open new interesting questions to be investigated.

For example, it would be possible to measure how the song repertoire of a population of agents would evolve if subjected to female agents that could positively or negatively select certain song features, such as conformity, complexity or novelty (Todd and Werner, 1999). In the case of novelty, it would be interesting to study, through the fine tuning of female choice, the level of novelty at which a male song could be attractive and positively selected and at what could be considered 'aberrant' and therefore not attractive, and what implication could this process have on song evolution and revolution at the population level (Frumhoff, 1983; Cerchio et al., 2001; Noad, 2002; Wiggins et al., 2015).

The agent-based model presented here has been developed as a purely cultural model, without the implementation of any sort of agent's fitness. However, the introduction of individual fitness, together with female agents and individual life histories could open horizons of new potential hypotheses to test. The model experiments of chapters 2 and 3 were run for a maximum of 10 migration cycles (i.e. 10

years); this time period represents a relatively short portion for a humpback whale with a potential life span of 95 years (Chittleborough, 1965). A future version of this model that accounted for individual life histories and fitness as well as processes of sexual selection through female preferences could be useful to test the role of conformity and novelty over evolutionary time scales, potentially contributing to the current debate about gene-culture coevolution and theoretical models of sexual selection (Mead and Arnold, 2004; Whitehead, 2017).

5.5.2. Song Production Algorithm

Another aspect of the model that could be improved is the song production algorithm. In the current model, agents were equipped with a first order Markov model with which they produced song sequences made of integer numbers through the use of a first order transition matrix, which I called a song representation (SR) in the chapters 2 and 3. First order Markov models have been shown to be inadequate in capturing the full complexity and hierarchical structure of humpback whale songs, where songs were represented as long string of units (Suzuki et al., 2006). On the other hand, if songs are represented as sequences of themes, then Markov models perform much more successfully, as recently demonstrated by Garland et al. (2017a). Therefore, even though the song sequences produced in these thesis experiments represented the theme sequences of humpbacks songs well; complexity at the phrase level, which also characterises humpback whale songs, was not properly represented.

A future song production algorithm that would aim to simulate humpback whale songs syntax both at the phrase and at the theme level would need to deal concurrently with unit/theme transition and unit/phrase repetition probabilities. While there are no studies that attempted to model humpback whale song syntax in its full complexity, other animal vocalisations, predominantly bird songs, have been investigated using a variety of syntax models (Berwick et al., 2011; Jin and Kozhevnikov, 2011; Katahira et al., 2011; Kershenbaum et al., 2014; Suzuki et al., 2016). One of the challenges in modelling humpback song sequences is the fact that, within each phrase, certain unit types are repeated several times consecutively while others are just repeated once, which poses a problem when phrases are modelled as probabilistic transitions between

units. A model approach that addressed this issue is the Partially Observable Markov Model with Adaptation (POMMA) designed by Jin and Kozhevnikov (2011) to model Bengalese finch (*Lonchura striata domestica*) songs syntax and to generate realistic renditions of these songs. The POMMA estimates for each unit type a repeat distribution curve based on observed data; this information is then used when generating sequences, when a unit transitions back to itself its transition probability varies as a function of the unit repeat number. Ideally, a syntax model that would seek to capture the whole hierarchical complexity of humpback whale song would be organised in two levels. The first would model the structure of phrases, using an approach similar to POMMA (Jin and Kozhevnikov, 2011) to reproduce probabilistically the unit combination of phrases and eventual unit repetition. This first level would be then nested within a second model level, which in this case could just be a first order Markov model, similar to the one already implemented in the current model architecture; this second model level would model the transition probabilities between the themes that constitute a song sequence. Although a model of this complexity would probably be computationally heavy, it could help elucidate with higher detail some of the potential mechanisms of song learning and evolution.

5.5.3. Applicability of this Modelling Framework to Other Species

As I explained at the beginning of this discussion, one of the main initial drivers of this thesis project was the interest to adapt the agent-based approach used to investigate the emergence of music to study the cultural evolution of humpback whales. Following the same interdisciplinary logic, the modelling effort to build the current model architecture has been directed towards making the model structure as modular as possible. During the analysis, this modularity allowed me to switch quickly between different learning biases, geographical and movement scenarios. However, this also means that the model could be adapted fairly easily to another target system, by substituting behavioural and environmental modules while maintaining the overall basic model structure. It would be interesting to adapt this versatile modelling framework to the study of other species' behavioural traits. The obvious candidates are species in which individuals produce vocalisations (or generally behavioural sequences) that could be modelled through a transition probability matrix and learned through social learning.

Furthermore, this modelling framework offers the opportunity to evaluate the effects of individuals' movement behaviour on individual and collective vocal learning and production. Among baleen whales, bowhead whales (*Balaena mysticetus*) have recently attracted interest due to their striking song production patterns, which show some similarities with humpback whales'. As with humpbacks, bowhead whale songs are thought be produced by males and likely function to mediate sexual competition and/or mating behaviours (Stafford et al., 2008; Johnson et al., 2015). Furthermore, even though the level of song complexity is lower, compared to humpbacks, the song type variability appears to be large, with novelty suggested as one of the potential drives of this extreme song diversity (Stafford et al., 2018). An agent-based model tailored to the ecology and peculiar environment of this inaccessible species could help create testable hypotheses about their acoustic behaviour and cognitive abilities. For decades, songbirds have been the gold standard for theoretical and empirical studies on song learning, song evolution and evolutionary processes relative to vocal behaviour. However, recent studies have shown that also other mammal species such as mice (*Scotinomys*), rock hyraxes (*Procavia capensis*), gibbons (*Hylobatidae*) and bats (*Chiroptera*) are able to produce complex vocal sequences, and these species could provide new interesting questions that an agent-based modelling approach like the one presented here could help answer (Davidson and Wilkinson, 2004; Clarke et al., 2006; Kershenbaum et al., 2012; Kershenbaum et al., 2014; Chabout et al., 2015).

5.6. Conclusions

Within the field of cultural evolution studies, theoretical models have played a fundamental role in providing researchers with testable hypotheses that helped progress the field at an incredibly fast pace. When properly informed with real data, theoretical models become extremely useful and efficient in uncovering the emergent characteristics of a system that, otherwise, would remain too complex to be explored empirically. The work presented in this thesis follows in the footsteps of the researchers that advanced, with their relentless efforts, the study of animal cultural evolution. Hopefully, some of the ideas and concepts developed here will contribute to the current discussion on animal social learning and will serve as inspiration for future colleagues

to keep collect valuable field data and to continue building increasingly complex and informative simulations of natural systems.

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Appendix 2

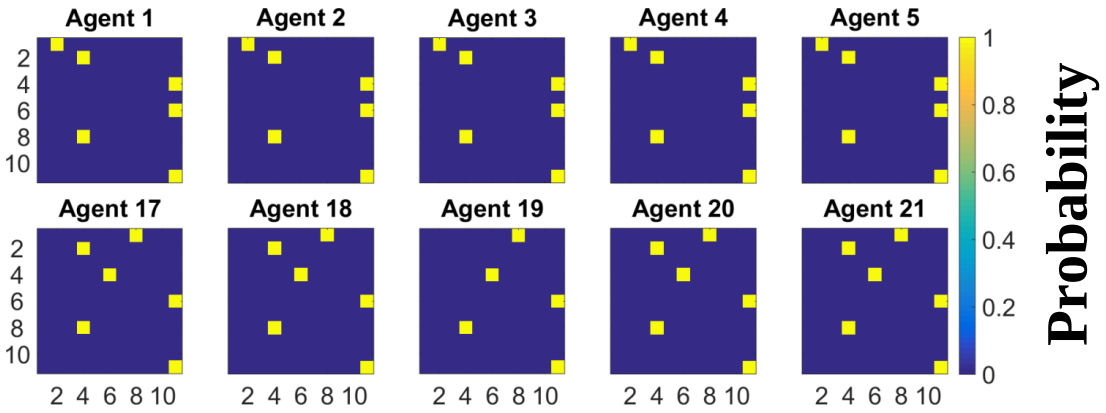

Figure A2.1. Example of SR matrices from a model 1 (distance-only) experiment. Agents 1-5 belong to population 1 while agents 17-21 belong to population 2. Transition probabilities are represented with different colours (see colour bar on the right-hand side). Theme number is indicated on the left-side and at the bottom of the SR matrices.

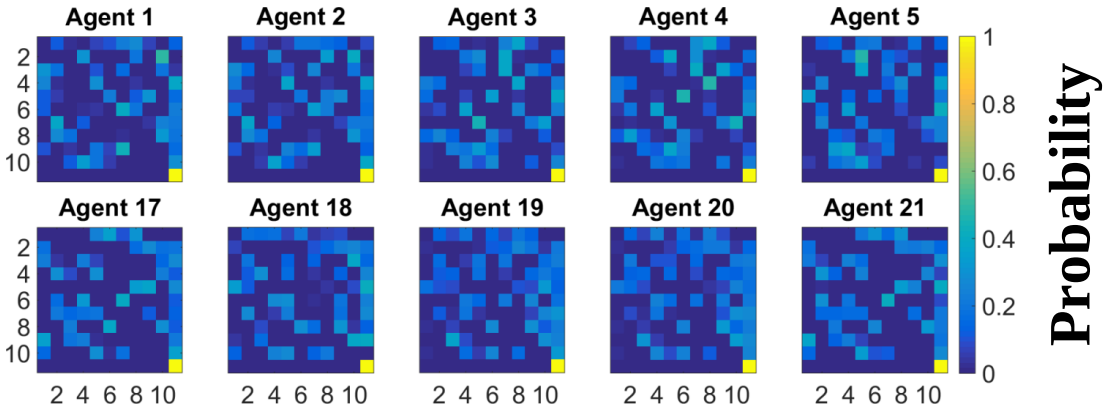

Figure A2.2. Example of SR matrices from a model 2 (distance + novelty) experiment. Agents 1-5 belong to population 1 while agents 17-21 belong to population 2. Transition probabilities are represented with different colours (see colour bar on the right-hand side). Theme number is indicated on the left-hand side and at the bottom of the SR matrices.

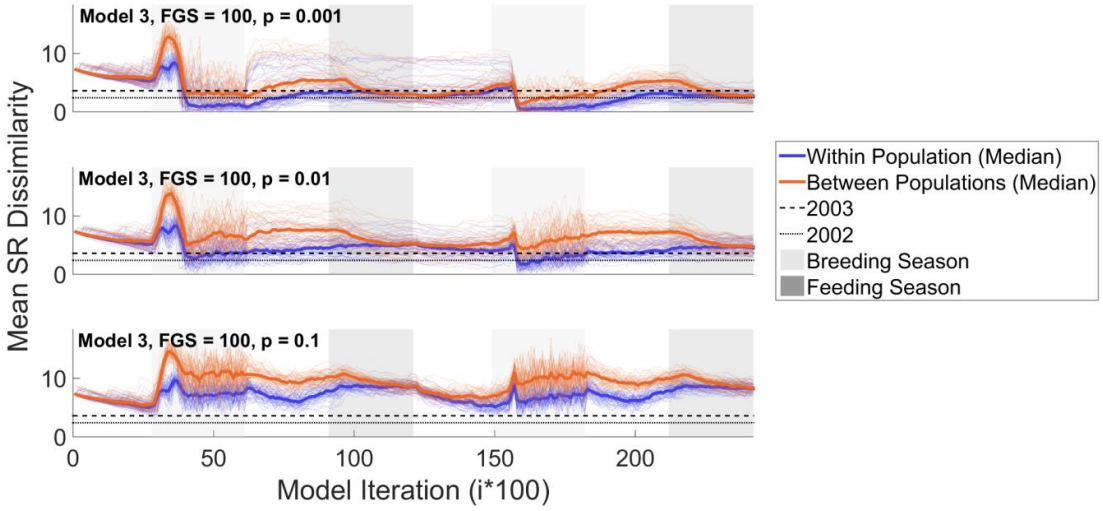

Figure A2.3. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 3. The upper panel shows the results for FGS = 100, P_e = 0.001, the middle panel shows the results for FGS = 100, P_e = 0.01 while the bottom panel shows the results for FGS = 100 and P_e = 0.1. The blue and orange coloured lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is showed with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

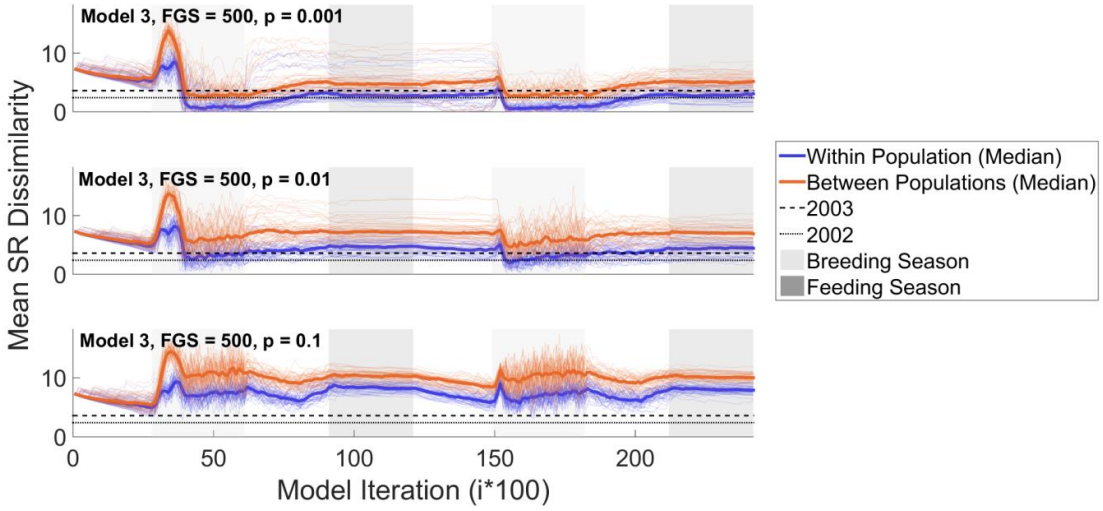

Figure A2.4. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 3. The upper panel shows the results for FGS = 500, P_e = 0.001, the middle panel shows the results for FGS = 500, P_e = 0.01 while the bottom panel shows the results for FGS = 500 and P_e = 0.1. The blue and orange coloured lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is showed with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

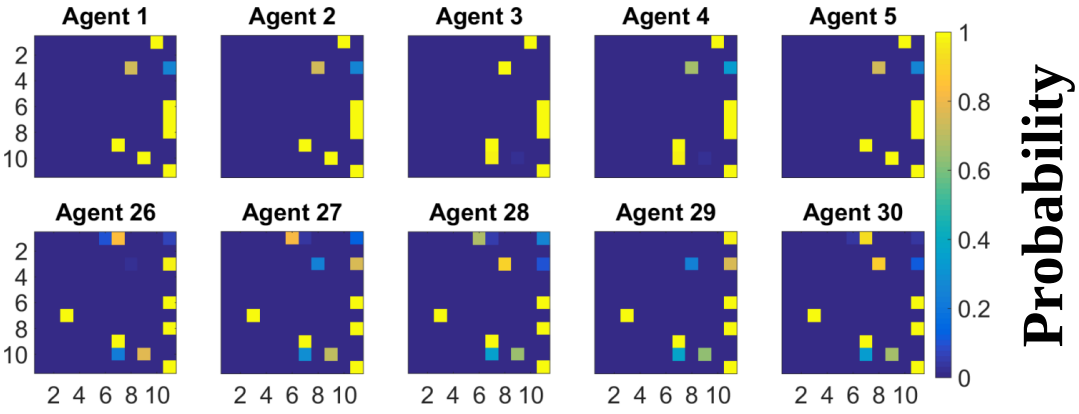

Figure A2.5. Example of SR matrices from a model 3 (distance + novelty + production error) experiment. Agents 1-5 belong to population 1 while agents 17-21 belong to population 2. Transition probabilities are represented with different colours (see colour bar on the right-hand side). Theme number is indicated on the left-hand side and at the bottom of the SR matrices.

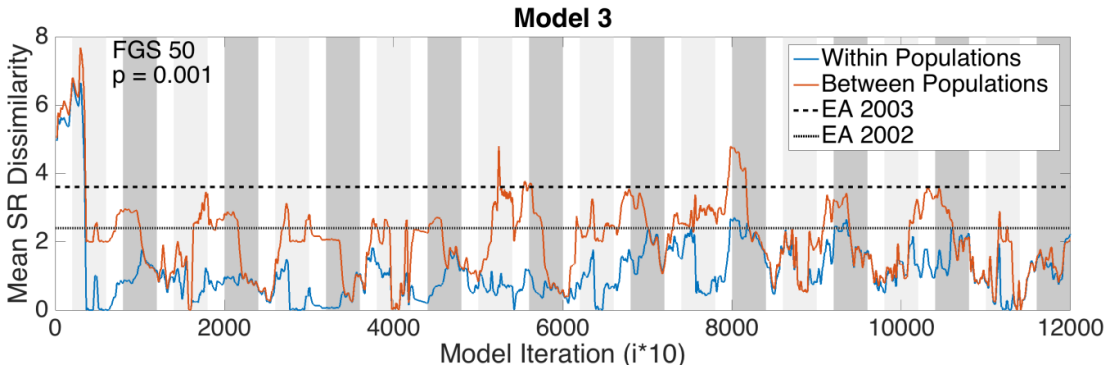

Figure A2.6. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 120,000, 10 migrations cycle) across the population of agents of model 3. The graph shows the results for FGS = 50, P_e = 0.001. The blue and orange coloured lines represent respectively within and between populations mean SR dissimilarity. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

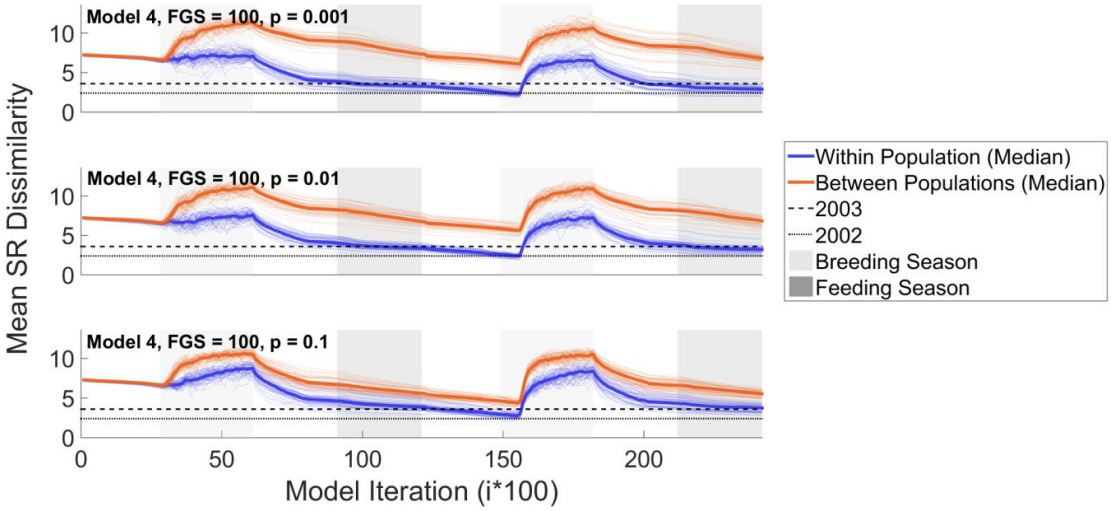

Figure A2.7. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 4. The upper panel shows the results for FGS = 100, P_e = 0.001, the middle panel shows the results for FGS = 100, P_e = 0.01 while the bottom panel shows the results for FGS = 100 and P_e = 0.1. The blue and orange coloured lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is showed with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

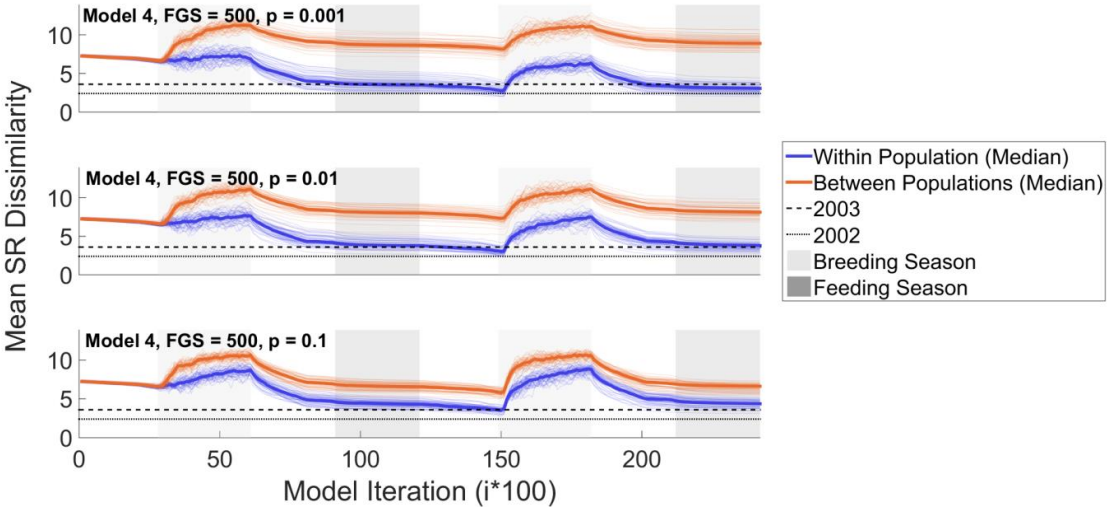

Figure A2.8. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 24,000) across the population of agents of model 4. The upper panel shows the results for FGS = 500, P_e = 0.001, the middle panel shows the results for FGS = 500, P_e = 0.01 while the bottom panel shows the results for FGS = 500 and P_e = 0.1. The blue and orange coloured lines represent respectively within and between populations mean SR dissimilarity. The median value for all the 50 modelling experiments (represented with thin lines) is showed with thick blue and orange lines. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia..

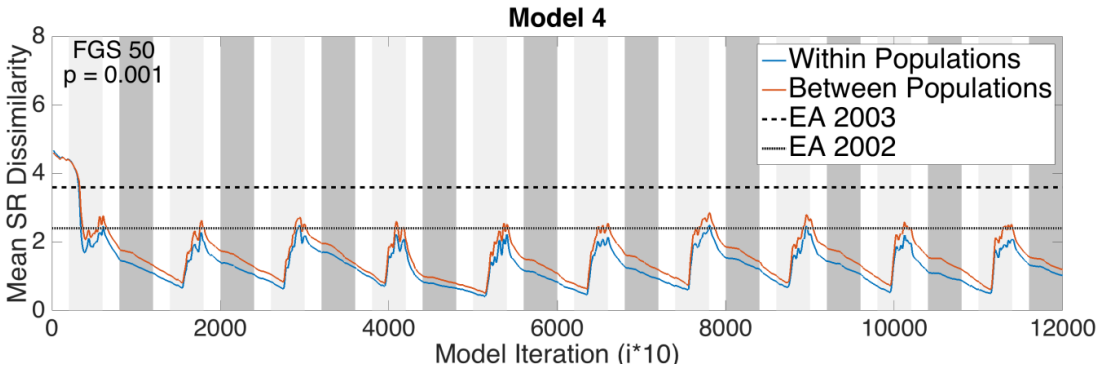

Figure A2.9. Mean SR dissimilarity calculated every 100th iteration (total number of iterations: 120,000, 10 migrations cycle) across the population of agents of model 4. The graph shows the results for FGS = 50, P_e = 0.001. The blue and orange coloured lines represent respectively within and between populations mean SR dissimilarity. The light and dark grey areas represent breeding and feeding seasons respectively. The horizontal dashed and dotted lines represent the mean SR dissimilarity estimates calculated respectively in 2002 and 2003, at the end of the breeding season in eastern Australia.

Appendix 3

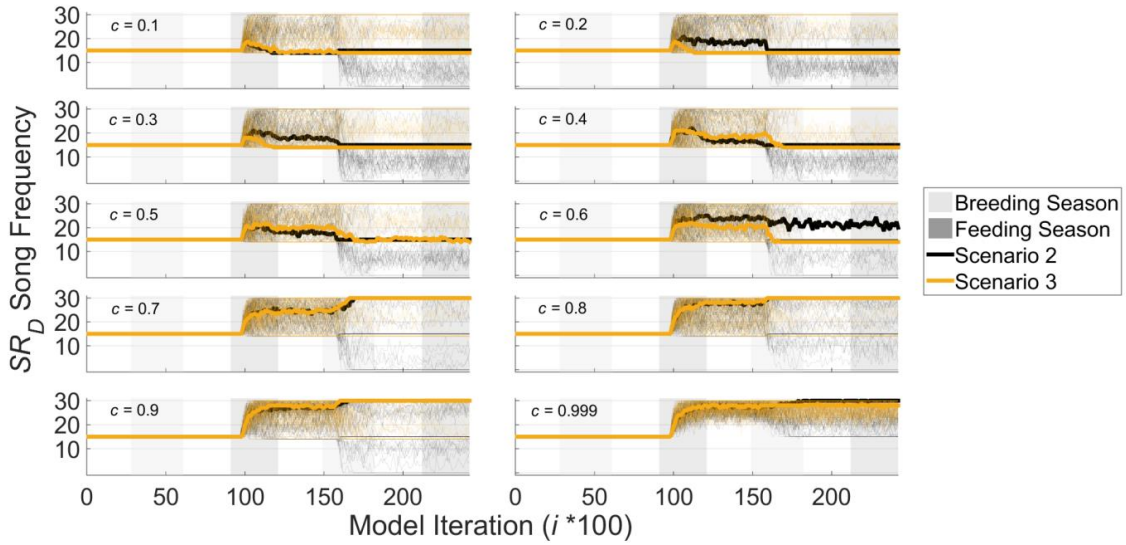

Figure A3.1. The effect of different values of memory conservativism (c) on SR_D song frequency compared between movement scenario 2 (black lines) and movement scenario 3 (yellow lines). Thick lines represent the median for each set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding ground was set to 5. The SR_D song frequency varied here between 0 and 30, comprising cumulatively all the agents from both populations, each formed by 15 agents respectively.

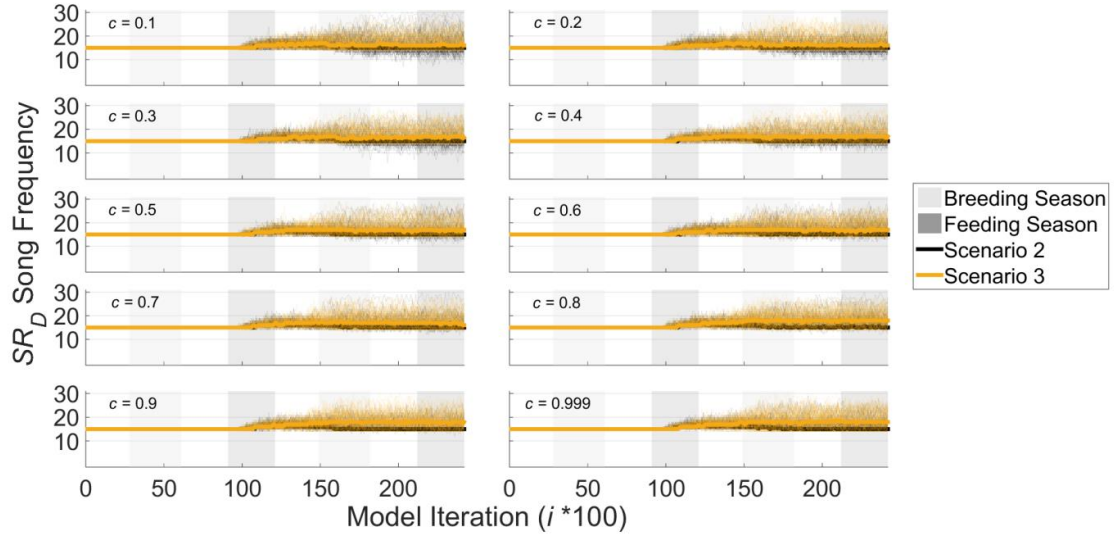

Figure A3.2. The effect of different values of memory conservativism (c) on SR_D song frequency compared between movement scenario 2 (black lines) and movement scenario 3 (yellow lines). Thick

lines represent the median for each set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding ground was set to 50. The SR_D song frequency varied here between 0 and 30, comprising cumulatively all the agents from both populations, each formed by 15 agents respectively.

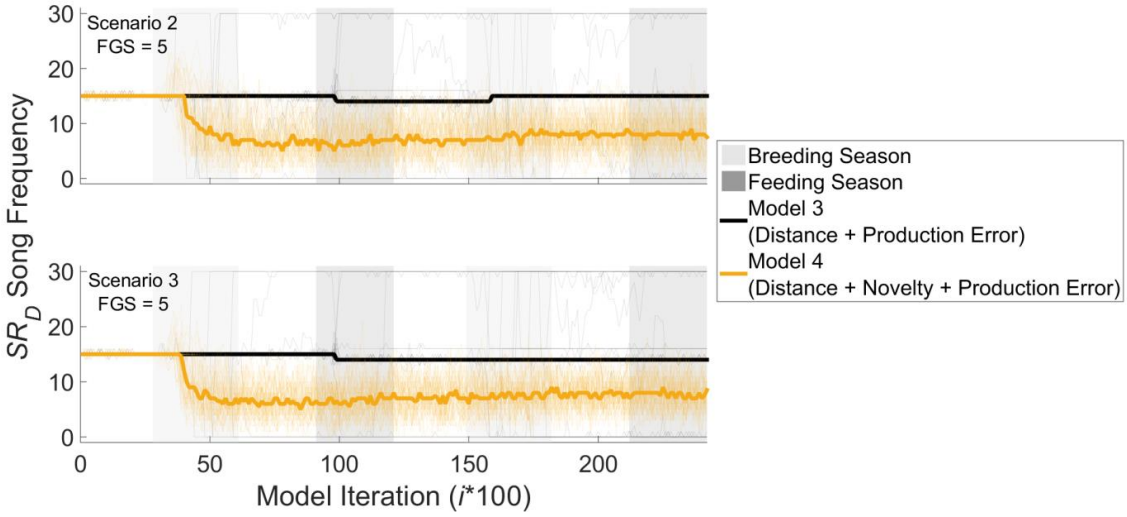

Figure A3.3. SR_D song frequency compared across two learning biases: distance + production error (model 3; black lines) and distance + novelty + production error (model 4, yellow lines). Thick lines represent the median for each learning bias set of 100 experiments (thin lines). The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding ground was set to 5. The SR_D song frequency varied here between 0 and 30, comprising cumulatively all the agents from both populations, each formed by 15 agents respectively.

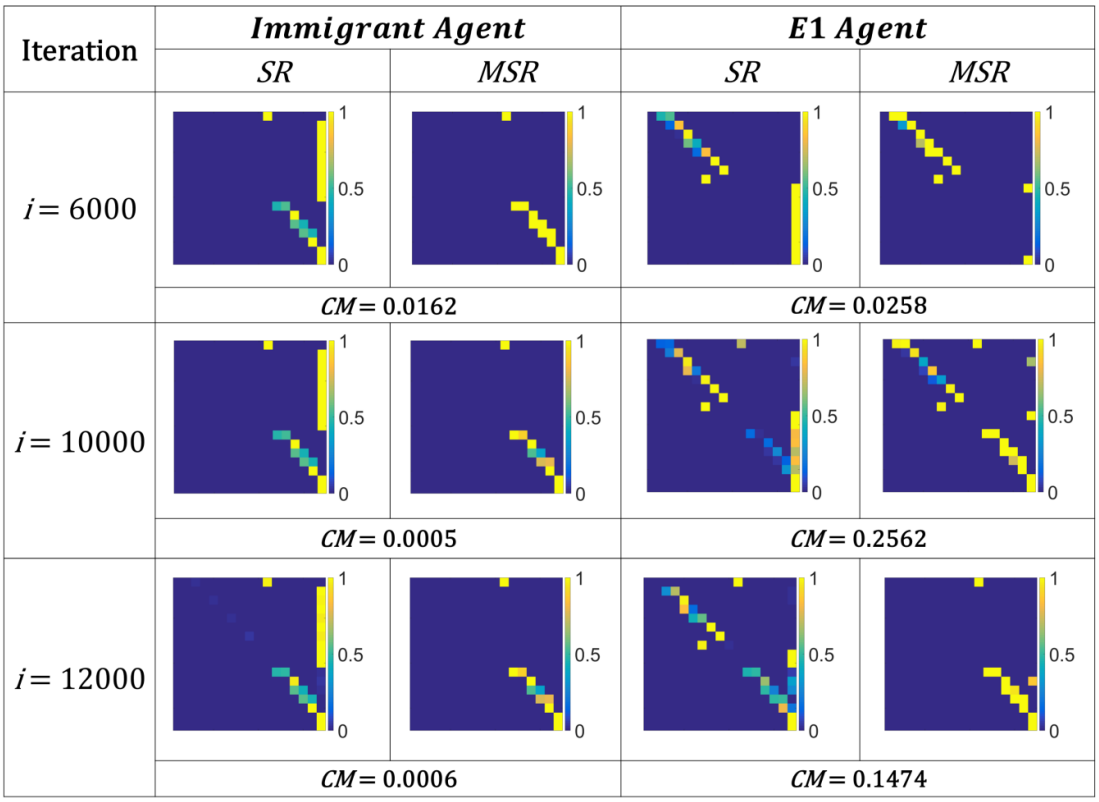

Figure A3.4. Example of conformity mismatch (*CM*) values for an immigrant and a resident agent of population E1 using their respective SR matrices and memory SRs (MSR). The respective SR, MSR and *CM* have been sampled at the end of the breeding season (first row), in the middle (middle row) and at the end (last row) of the feeding season. (Note that due to the fact that MSRs are multiplied by the singers' intensity factors, their transition probabilities are usually low and here to increase the graphical clearness of these examples I used MSRs with unrealistically high transition probabilities).

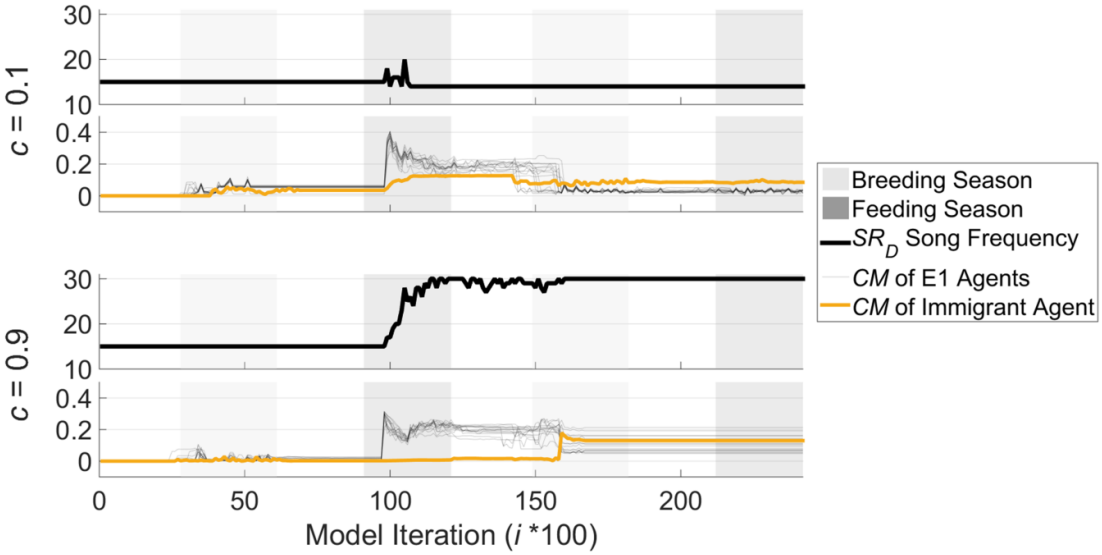

Figure A3.5. Comparison between SR_D song frequency (thick black lines) and individual conformity mismatch trends (*CM*; thin black lines for agents of population E1, thick yellow line for the immigant agent) in two model experiments of movement scenario 3 that presented different levels of memory conservatism (c = 0.1, top panels; c = 0.9, bottom panels). The light and dark grey areas represent breeding and feeding seasons respectively. The size of the breeding and feeding ground was set to 5. The SR_D song frequency varied here between 0 and 30, comprising cumulatively all the agents from both populations, each formed by 15 agents respectively.

Appendix 4

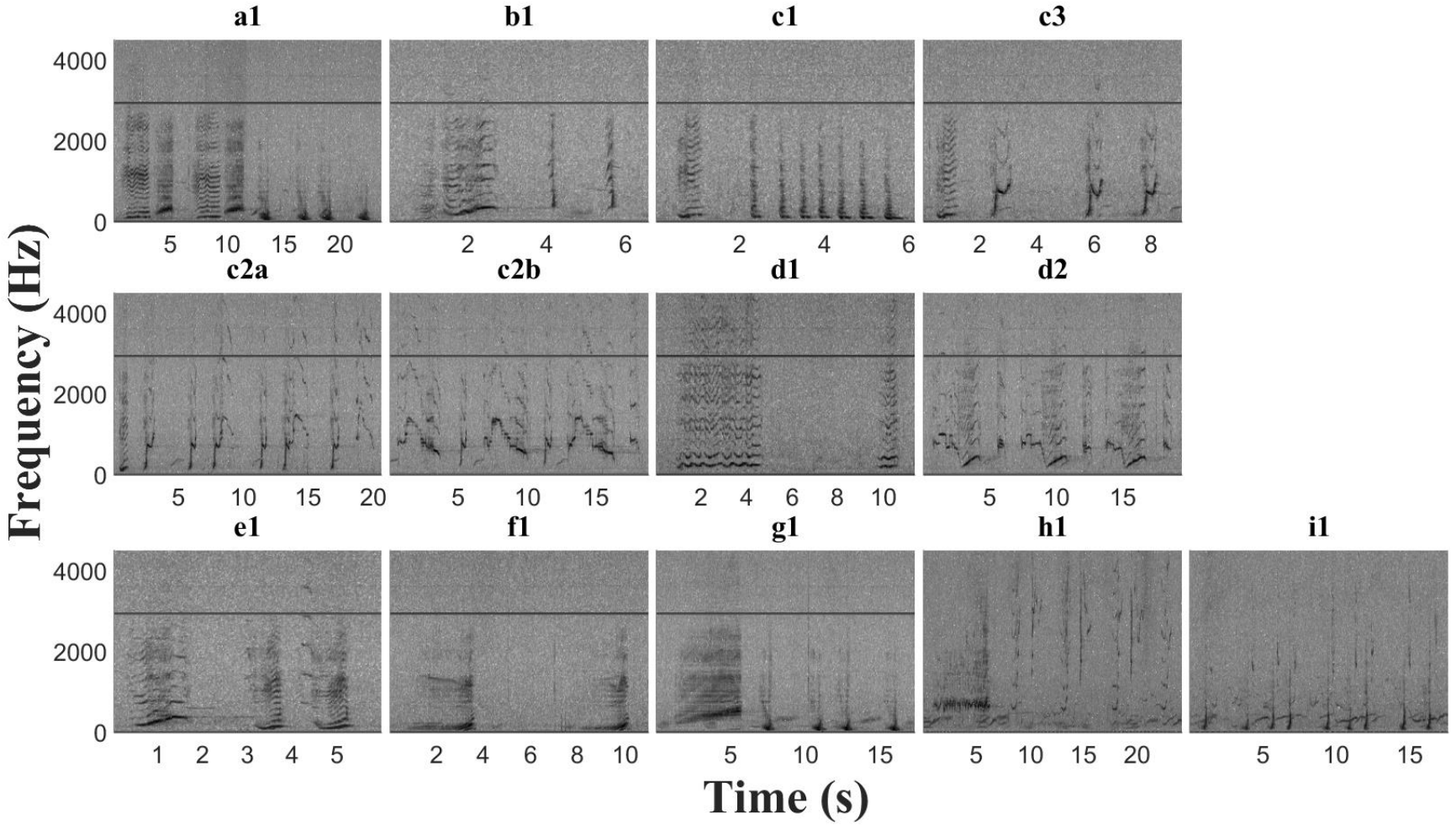
a1
b1
c1
c3
c2a
c2b
d1
d2
e1
f1
g1
h1
i1
Frequency (Hz)
4000
2000
0
Time (s)

Figure A4.1. Spectrograms of representative sub-phrases for 2002 song type. Spectrogram parameters: Hann window, window size: 1024; 50% overlap. Sub-phrase a1: (‘modulated moan’ [MM] + ‘purr’ [PPR] or ‘trill’ [TRR] x 2 + ‘croaks’ [CRK] x 4. Sub-phrase b1: ‘modulated or ascending moan’ [MM or AM] + ‘whoop’ [WO] x 2. Sub-phrase c1: ‘ascending moan’ [AM] + ‘grunt’ [GR] x 6-8. Sub-phrase c3: ‘ascending moan’ [AM] + ‘trumpet’ [TR] x 3. Sub-phrase c2: ‘ascending moan’ [AM] + ‘trumpet’ [TR] x 3 + ‘N-shaped shriek’ [NSH] + ‘trumpet’ [TR] x 2 + ‘N-shaped shriek’ [NSH] + ‘trumpet’ [TR] + ‘N-shaped shriek’ [NSH]. Sub-phrase d1: ‘siren’ [SI] + ‘mini-siren’ [MSI]. Sub-phrase d2: (‘N-shaped shriek’ [NSH] + ‘ascending moan’ [AM] + ‘short shriek’ [SSH]) x 3. Sub-phrase e1: ‘ascending moan’ [AM] + ‘violin’ [VI] x 2. Sub-phrase f1: ‘long bark’ [LBA] + ‘bark’ [BA]. Theme g1: ‘bellow’ [BLW] + ‘croaks’ [CRK] x 4. Sub-phrase h1: ‘eee’ [E] + (‘ascending shriek’ [ASH] + ‘modulated whistle’ [MW]) x 4. Sub-phrase i1: (‘whoop’ [WO] + ‘bird whistle’ [BW]) x 9.

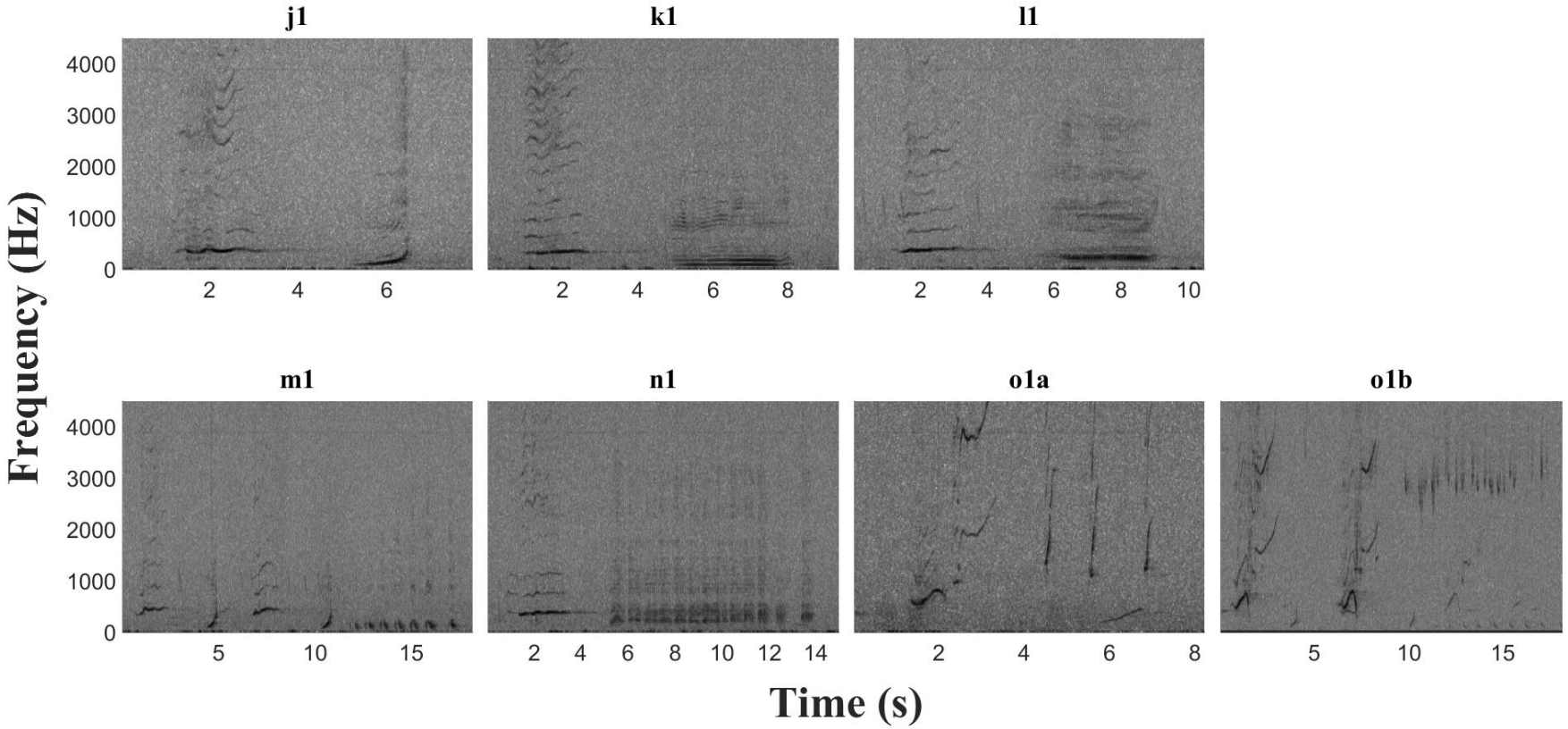

Figure A4.2. Spectrograms of representative sub-phrases for 2003 song type. Spectrogram parameters: Hann window, window size: 1024; 50% overlap. Sub-phrase j1: 'modulated moan' [MM] + 'bark' [BA]. Sub-phrase k1: 'modulated moan' [MM] + 'long bark' [LBA]. Sub-phrase l1: 'modulated moan' [MM] + 'long growl' [LGO]. Sub-phrase m1: ('modulated moan' [MM] + 'bark' [BA]) x 2 + 'grunts' [GR] x 5-7. Sub-phrase n1: 'modulated moan' [MM] + 'ratchet' [RA] x 10-12. Sub-phrase o1a: 'high modulated moan' [HMM] + 'high shriek' [HSH] + 'high squeak' [HSQ] x 2-3. Sub-phrase o1b: 'high modulated moan' [HMM] + 'high shriek' [HSH] x 2 + 'bird whistle' [BW] x 5-10.

Table 4.1. 2002 sub-phrase median strings computed for each individual with LD analysis.

Sub-Phrase	ID	Median Sequence
a1	13	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	14	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	15	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	16	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	19	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	20	MM, PRR, MM, PRR, CRK, CRK, CRK
	21	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	22	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	23	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	24	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	25	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	26	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
	27	MM, PRR, MM, PRR, CRK, CRK, CRK, CRK
b1	13	MM, WO, WO
	14	MM, WO, WO
	15	AM, WO, WO
	16	AM, WO, WO
	19	AM, WO, WO
	20	AM, WO, WO
	21	AM, WO, WO
	22	AM, WO, WO
	23	AM, WO, WO
	24	AM, WO, WO
	25	AM, WO, WO
	26	MM, WO, WO
	27	AM, WO, WO
c1	13	AM, GR, GR, GR, GR, GR, GR
	14	GR, GR, GR, GR, GR, GR, GR, GR, GR, GR, GR, GR
	15	AM, GR, GR, GR, GR, GR, GR
	16	AM, GR, GR, GR, GR, GR
	19	AM, GR, GR, GR, GR, GR
	20	AM, GR, GR, GR, GR, GR, GR
	21	AM, GR, GR, GR, GR, GR, GR
	22	AM, GR, GR, GR, GR, GR, GR
	23	AM, GR, GR, GR, GR, GR
	24	AM, GR, GR, GR, GR, GR, GR
	25	AM, GR, GR, GR, GR, GR, GR, GR
	26	AM, GR, GR, GR, GR, GR, GR
	27	AM, GR, GR, GR, GR, GR, GR, GR, GR, GR, GR
c2a	13	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH, TR, NSH
	14	TR, TR, TR, TR, NSH, TR, NSH, TR, NSH, TR, NSH
	15	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH, TR, NSH
	16	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH, TR, NSH
	19	AM, TR, TR, NSH, TR, NSH, TR, NSH, TR, NSH
	20	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH, TR, NSH
	21	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH, DC, TR, NSH
	22	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH, TR
	23	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, NSH, TR, NSH
	24	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH, TR, NSH
	25	AM, TR, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH
	26	AM, TR, TR, TR, NSH, TR, TR, NSH, DC, TR, TR, NSH, TR, NSH
	27	AM, TR, NSH, TR, TR, NSH, TR, TR, NSH, TR, TR, NSH
c2b	13	TR, NSH, DC, TR, TR, NSH, DC, TR, NSH, DC, TR, NSH
	14	NSH, DC, TR, NSH, DC, TR, NSH, DC, NSH
	15	NSH, DC, TR, NSH, DC, TR, NSH, DC, NSH
	16	NSH, DC, TR, NSH, DC, TR, NSH, DC, NSH
	19	NSH, DC, TR, NSH, DC, TR, NSH, DC, NSH
	20	NSH, DC, SSH, NSH, DC, SSH, NSH, DC, SSH
	21	TR, NSH, DC, TR, NSH, AM, SSH, NSH, AM, SSH
	22	
	23	TR, NSH, DC, TR, NSH, DC, TR, NSH, DC, NSH
	24	NSH, TR, NSH, DC, TR, NSH, DC, TR, NSH
	25	NSH, DC, TR, NSH, DC, TR, NSH, DC, NSH
	26	NSH, DC, TR, NSH, DC, SSH, NSH, AM, SSH
	27	
c3	13	AM, TR, TR, TR
	14	TR, TR, TR
	15	AM, TR, TR, TR
	16	AM, TR, TR, TR
	19	AM, TR, TR, TR, TR
	20	AM, TR, TR, TR
	21	AM, TR, TR, TR
	22	AM, TR, TR, TR
	23	AM, TR, TR, TR
	24	AM, TR, TR, TR
	25	AM, TR, TR, TR
	26	AM, TR, TR, TR
	27	AM, TR, TR
d1	13	SI, MSI
	14	SI, MSI
	15	SI, MSI
	16	SI, MSI
	19	SI, MSI
	20	SI, MSI
	21	SI, MSI
	22	SI, MSI
	23	SI, MSI
	24	SI, MSI
	25	SI, MSI
	26	SI, MSI
	27	SI, MSI
d2	13	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, NSH
	14	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	15	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	16	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	19	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	20	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	21	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	22	NSH, AM, TR, NSH, AM, TR, NSH, AM, SSH
	23	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	24	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	25	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	26	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
	27	NSH, AM, SSH, NSH, AM, SSH, NSH, AM, SSH
e1	13	AM, VI, VI
	14	AM, VI, VI
	15	AM, VI, VI
	16	AM, VI, VI
	19	AM, VI, VI
	20	AM, VI, VI
	21	AM, VI, VI
	22	AM, VI, VI
	23	AM, VI, VI
	24	AM, VI, VI
	25	AM, VI, VI
	26	AM, VI, VI
	27	AM, VI, VI
f1	13	LBA, BA
	14	LBA, BA
	15	LBA, BA
	16	LBA, BA
	19	LBA, BA
	20	LBA, MSI
	21	LBA, BA
	22	LBA, BA
	23	LBA, BA
	24	LBA, BA
	25	LBA, BA
	26	LBA, BA
	27	LBA, BA
g1	13	BLW, CRK, CRK, CRK, CRK
	14	BLW, CRK, CRK, CRK, CRK
	15	BLW, CRK, CRK, CRK, CRK
	16	BLW, CRK, CRK, CRK, CRK
	19	BLW, CRK, CRK, CRK, CRK
	20	BLW, CRK, CRK, CRK
	21	BLW, CRK, CRK, CRK, CRK
	22	BLW, CRK, CRK, CRK, CRK
	23	BLW, CRK, CRK, CRK, CRK
	24	BLW, CRK, CRK, CRK, CRK
	25	BLW, CRK, CRK, CRK, CRK
	26	BLW, CRK, CRK, CRK, CRK
	27	BLW, CRK, CRK, CRK, CRK
i1	14	WO, BW
h1	14	ASH, MW, ASH, MW, ASH, MW, ASH, E

Table A4.2. 2003 sub-phrase median strings computed for each individual with LD analysis.

Sub-Phrase	*ID*	*Median Sequence*
j1	1	*MM, BA*
	2	*MM, BA*
	3	*MM, BA*
	4	*MM, BA*
	5	*MM, BA*
	6	*MM, BA*
	7	*MM, BA*
	8	*MM, BA*
	9	*MM, BA*
	10	*MM, BA*
	12	*MM, BA*
	17	*MM, BA*
k1	1	*MM, LBA*
	2	*MM, LBA*
	3	*MM, LBA*
	4	*MM, LBA*
	5	*MM, LBA*
	6	*MM, LBA*
	7	*MM, LBA*
	8	*MM, LBA*
	9	*MM, LBA*
	10	*MM, LBA*
	12	*MM, LBA*
	17	*MM, LBA*
l1	1	*MM, LGO*
	2	*MM, LGO*
	3	*MM, LGO*
	4	*MM, LGO*
	5	*MM, LGO*
	6	*MM, LGO*
	7	*MM, LGO*
	8	*MM, LGO*
	9	*MM, LGO*
	10	*MM, LGO*
	12	*MM, LGO*
	17	*MM, LGO*
m1	1	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR*
	2	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR*
	3	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR*
	4	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR, GR*
	5	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR*
	8	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR*
	9	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR*
	10	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR*
	12	*MM, BA, MM, BA, GR, GR, GR, GR, GR, GR, GR, GR, GR, GR*

Sub-Phrase	*ID*	*Median Sequence*
n1	1	*MM, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	2	*MM, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	3	*MM, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	4	*MM, MM, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	5	*MM, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	8	*MM, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	9	*MM, MM, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	10	*MM, MM, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA*
	12	*MM, MM, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA, RA*
o1a	1	*HMM, HSH, HSQ, HSQ*
	2	*HMM, HSH, HSQ*
	3	*HMM, HSH, HMM, HSH, HSQ*
	4	*HMM, HSH, HSQ*
	5	*HMM, HSH, HSQ*
	8	*HMM, HSH, HMM, HSH, HSQ, HSQ*
	12	*HMM, HSH, HSQ*
	17	*HMM, HSH, HMM, HSH, HSQ, HSQ*
o1b	1	*HMM, HSH, HMM, HSH, BW, BW, BW, BW, BW*
	2	*HMM, HSH, HMM, HSH, BW, BW, BW, BW, BW*
	3	*HMM, HSH, HMM, HSH, BW, BW, BW, BW, BW*
	4	*HMM, HSH, HMM, HSH, BW, BW, BW, BW, BW, BW, BW, BW*
	5	*HMM, HSH, HMM, HSH, BW, BW, BW, BW, BW, BW, BW*
	8	*HMM, HSH, HMM, HSH, BW, BW, BW, BW*
	12	*HMM, HSH, HMM, HSH, BW, BW, BW, BW, BW*
	17	*HMM, HSH, HMM, HSH, BW, BW, BW, BW, BW, BW, BW, BW, BW, BW, BW*

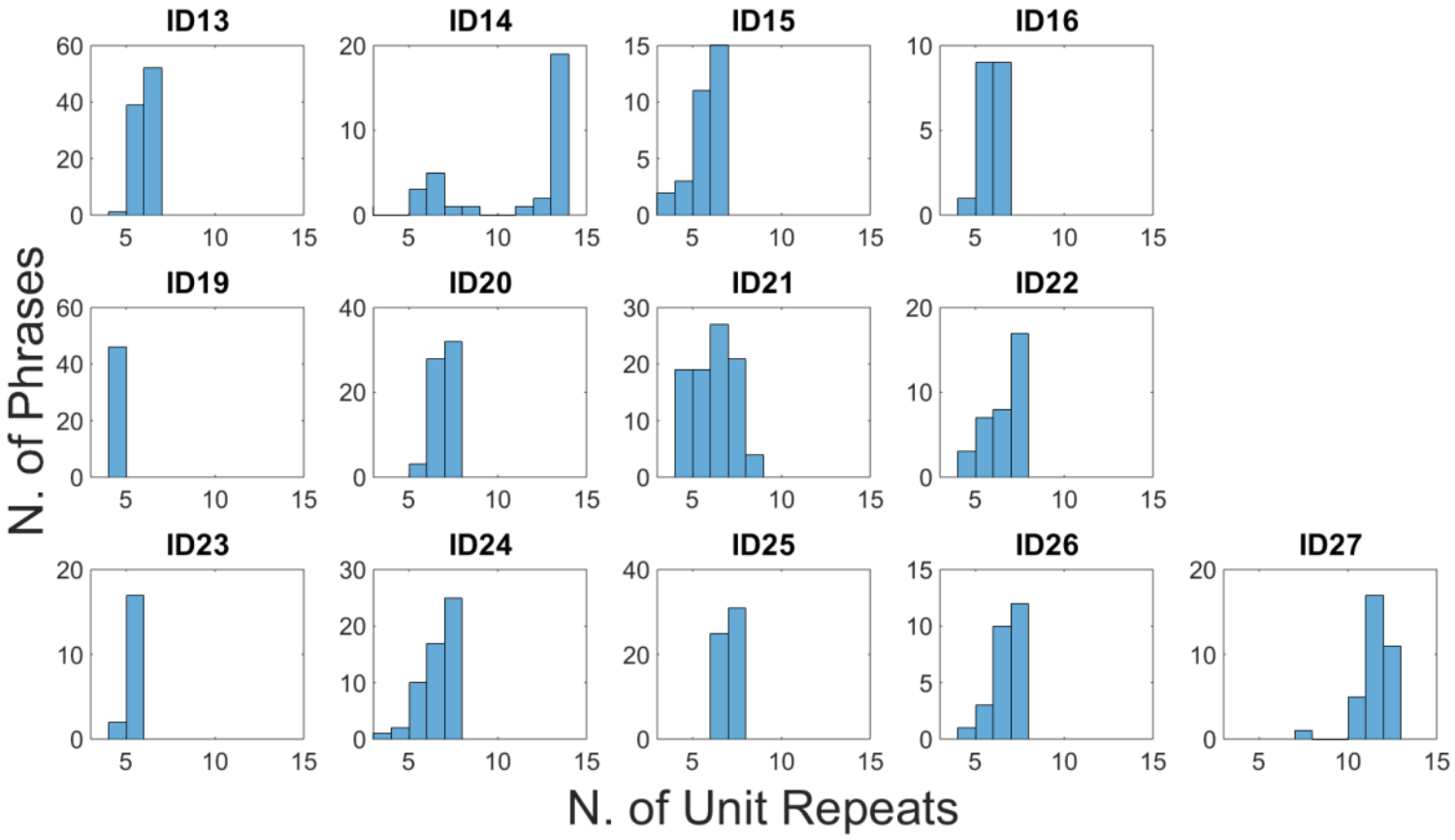

Figure A4.3. 'Grunts' (GR) repeat distribution within c1 sub-phrases computed for each individual.

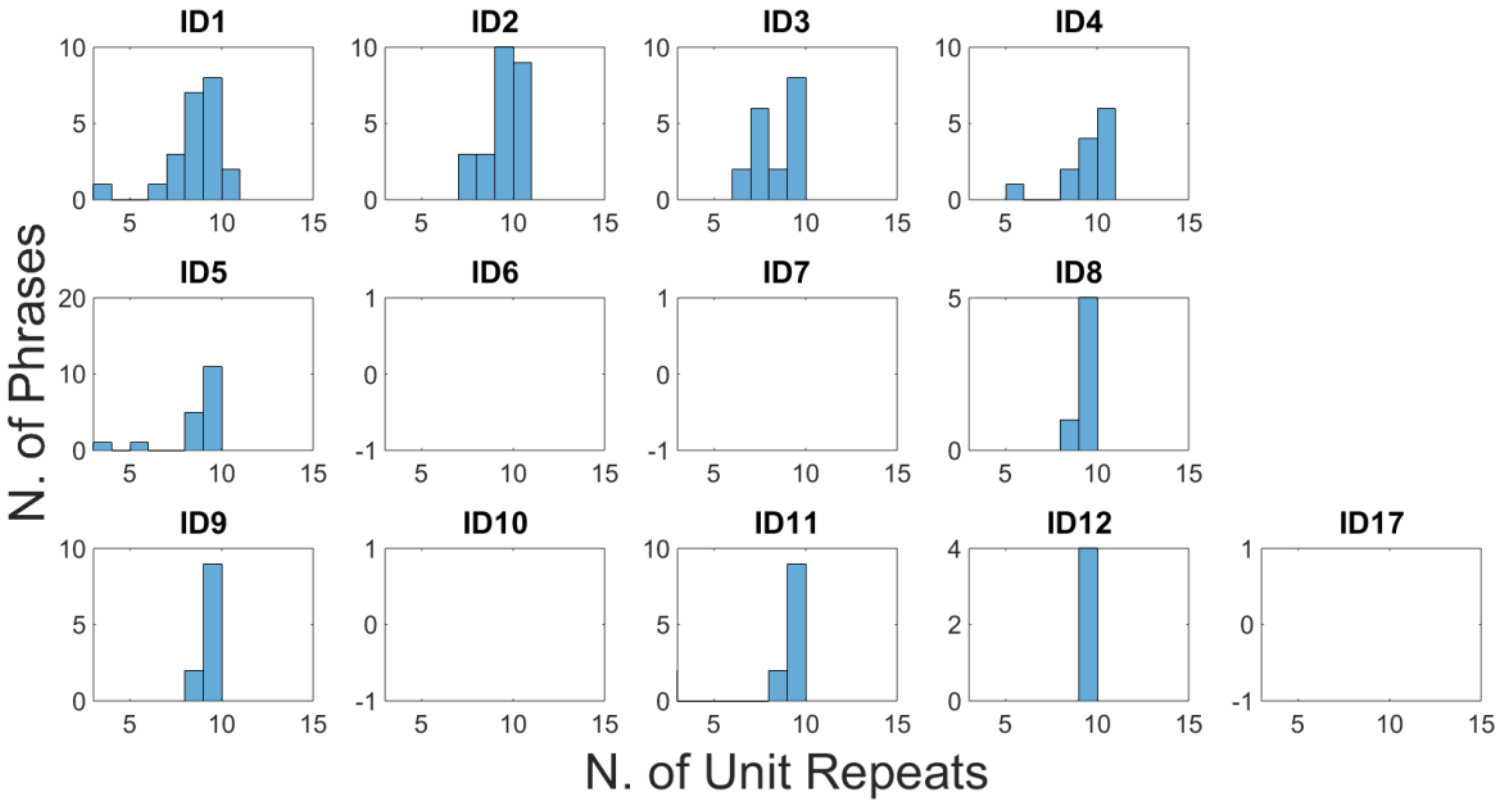

Figure A4.4. 'Grunts' (GR) repeat distribution within d1 sub-phrases computed for each individual.